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Fishery Bulletin

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Fishery Bulletin

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INFLUENCE OF WATER CURRENTS AND ZOOPLANKTON DENSITIES ON DAILY FORAGING MOVEMENTS OF BLACKSMITH, *CHROMIS PUNCTIPINNIS*, A PLANKTIVOROUS REEF FISH

RICHARD N. BRAY[1]

ABSTRACT

The blacksmith, *Chromis punctipinnis*, one of the most abundant fishes in kelp forests off southern California, daily emerges from rock shelters and moves to specific locations where it forages in the midwater on zooplankton. Midwater transects taken over a reef that experiences occasional reversals in water currents indicated that large blacksmith (greater than 150 mm total length) consistently gathered at the incurrent end of the reef. These movements are probably related to the availability of food. Replicate plankton tows taken near the ends of the reef demonstrated that zooplankton densities were greater at the incurrent end. Experiments in which large fish were placed in cages suspended in midwater at both reef ends demonstrated that individuals foraging at the incurrent end consumed more prey. Small blacksmith (less than 125 mm total length) did not undergo foraging movements. Instead, most remained in the shallower portions of the reef, close to cover, even though caging experiments and collections of free-living individuals indicated that these fish would consume more prey if they moved upcurrent. Since small as well as large blacksmith benefit from foraging at the incurrent end, the size-specific differences in foraging movements probably reflect differences in the cost of migrating in terms of time, energy, and predation.

Many fishes on temperate and tropical reefs feed heavily on zooplankton. They eat either by day or by night, and school or shelter when inactive (Hobson 1972, 1973, 1974; Hobson and Chess 1976). Some planktivores limit their movements to the water column above their shelters (e.g., Sale 1971; Hobson 1972, 1973); the distribution and small-scale movements of these parochial species have been the subject of recent quantitative investigations (e.g., Stevenson 1972; Hobson and Chess 1978; de Boer 1978). Other planktivores undergo extensive horizontal movements (Hobson 1972, 1973), and have received less attention. Nonetheless, migrating planktivores are often extremely abundant and probably import substantial amounts of extrinsic energy—drift zooplankton—into reef communities (Stevenson 1972).

The blacksmith, *Chromis punctipinnis*, a planktivorous pomacentrid that may grow to a total length (TL) of 300 mm (Miller and Lea 1972), is one of the most abundant fishes inhabiting the inshore rocky reefs of southern California. In aggregations of up to several hundred individuals, they feed throughout the day on a variety of zooplankton, including larvaceans, copepods, cladocerans, and various larvae (Hobson and Chess 1976). At dusk, they descend to the reef surface where they shelter in holes and crevices until dawn (Ebeling and Bray 1976; Hobson and Chess 1976). Many tropical congeners of the blacksmith have similar activity patterns (e.g., Hobson 1965, 1972; Collette and Talbot 1972; Emery 1973).

During preliminary observations on rocky reefs near Santa Barbara, Calif., I found that blacksmith often forage and shelter in different areas. Large numbers of blacksmith emerge from shelters at dawn, assemble into a school, and move to a location above a reef, where they disperse into a loose aggregation in the midwater and forage on zooplankton. At least some blacksmith near Santa Catalina Island, Calif., show a similar pattern (Hobson and Chess 1976). In commenting on the location of daytime foraging aggregations, Limbaugh (1955) observed that, "Thick schools of young to half-grown blacksmith often form where a plankton-rich current enters the kelp bed." Such a response to water currents would enable blacksmith to be among the first of many vertebrate and invertebrate planktivores to forage on plankton as it is swept across the reef community. However,

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other factors may also affect the distribution of blacksmith. For example, kelp and high relief rocks may serve as orientation points or shelter for fish in the water column (Limbaugh 1955; Quast 1968a, b, c; Ebeling and Bray 1976; Hobson and Chess 1976).

In this paper, I first examine the distribution of blacksmith in relation to water currents over a reef that is subjected to occasional reversals in current flow to see if they consistently gather at the incurrent end. Since foraging is the major activity of blacksmith while assembled in these midwater aggregations, I then determine if plankton is more abundant at the incurrent end. Finally, by examining caged and free-living individuals, I see whether blacksmith that forage at the incurrent end consume more prey.

METHODS

Study Site

Naples Reef is a large rocky outcrop (275 × 80 m) located 24 km west of Santa Barbara and 1.6 km offshore (Figure 1). The substratum is a series of uplifted sandstone rills and ridges that parallel the coast. Depths across the reef average 8-10 m, although some prominences come to within 5 m of the surface. A sandy bottom 16-20 m deep surrounds the reef, with rocky outcrops inshore and cobbles offshore. The assemblage of plant and animal life on and around the reef is among the richest along the Santa Barbara coast. Giant kelp, *Macrocystis pyrifera*, is always present on the reef, although kelp densities fluctuated considerably throughout the study period. The species composition and abundance of fishes at Naples Reef are listed in Ebeling et al. (1980).

Naples Reef is well suited to study the effects of water currents on the distribution of fish. The reef is almost always swept by measurable longshore currents. Although usually these come from the east, occasionally they come from the west. A shift in the distribution of fish when the currents reverse would provide strong evidence that water currents affect the fish's distribution.

Surveys

In December 1975, I initiated biweekly counts of all fish in the water column at four sites on the reef (Figure 1). At each site, I fixed a line from a

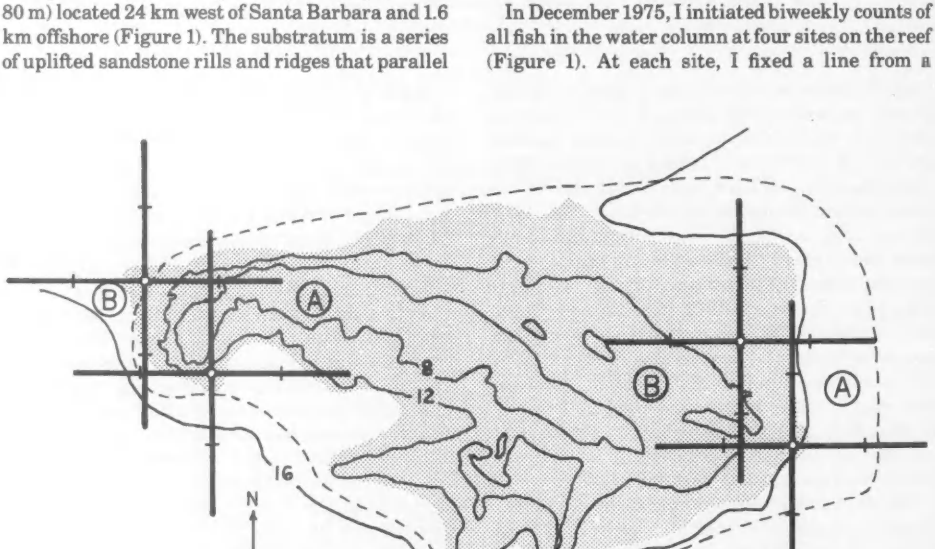

FIGURE 1.—Contour map of Naples Reef, southern California. Heavy lines indicate locations of midwater transects: 30 m (to cross mark) and 60 m (to end) from the starting points (circles). Letters indicate incurrent and excurrent locations where zooplankton were sampled: A locations—when current flowed from the east; B locations—when current flowed from the west. Midwater cages were located at the A locations. The shaded portion indicates the rocky substratum, while the surrounding open area represents sand. The dashed line indicates the margin of the kelp bed. Depths are in meters.

permanent anchoring point to a buoy within 1 m of the surface. At middepth (6 m), I attached a transect line and swam four transects at a constant speed, one each to the north, east, south, and west. Without moving my head, I counted all blacksmith within my field of view. Fish were tallied in separate columns on a slate according to their size as estimated by eye: juveniles (<125 mm TL), halfgrown fish (125-150 mm), and adults (>150 mm). These classes refer to sizes and not necessarily to stages of sexual maturity. A complete survey consisted of 16 transects: 4 at each of the four sites on the reef. During the first 26 surveys (9 December 1975-2 November 1976), the length of the transect line was 30 m, so a total of 480 m were traversed each survey. For the remaining 13 surveys (9 November 1976-23 July 1977), the length of the transects was doubled to 60 m each (960 m/survey) to see if large aggregations of blacksmith occurred beyond the areas that were initially sampled. I did not conduct surveys when visibility was <2 m.

I also examined several oceanographic variables at each site on the reef. Water visibility was measured during each transect as the distance at which I could easily discern a fishlike silhouette attached to the line. Water velocities were measured several times at each site by timing the movement of small particles. And surface, midwater, and bottom water temperatures were taken with a small dial thermometer.

Plankton Sampling

Once the movements of blacksmith were determined, I made replicate zooplankton tows at known sheltering sites near the excurrent end of the reef, and known foraging sites at the incurrent end. Incurrent samples were collected at the margin of the kelp bed, over the sand bottom that surrounds the reef. Excurrent samples were taken within the bed, above rocky areas that provide shelter for large numbers of blacksmith at night. The exact location of the sample sites depended on the direction of the water currents (Figure 1). I specifically avoided sampling on days when the current velocity was negligible, when there were obvious eddies, or when the current flow was not along the east-west axis of the reef.

Plankton were collected between 1000 and 1400 h with a 0.5 m diameter 0.333 mm mesh net pushed by a diver. A TSK[2] flowmeter, fitted across the net opening, measured the filtered volume of water. I randomized (by coin flip) my choice of which end to sample first, thereby restricting such variables as collection time, net clogging, diver fatigue, etc., to random error. Each tow was double oblique, going from the surface to a depth of 6 m, then back to the surface. The diver swam a haphazard pattern through the kelp bed and avoided sampling within 1 m of a kelp plant or the bottom. All samples were immediately fixed in 5% buffered Formalin. The time interval between the first and last tows in a collection ranged from 1.5 to 4.5 h.

In the laboratory, samples were split with a Folsum plankton splitter: one-half was used for weighing and the other half was used for counting. For dry weights, samples were filtered (vacuum pressure = 725 mm Hg) onto preweighed GF/C filters, and dried at 60° C to a constant weight. For counting, samples were split two more times, then subsampled with three 10 ml aliquots drawn with a Stemple pipette. The plankton were counted under a dissecting microscope and sorted into broad taxonomic categories. Weights and counts were standardized by conversion to amounts per cubic meter of water sampled.

I analyzed the data in two ways to compare densities of zooplankton between incurrent and excurrent ends of the reef. First, I compared the individual incurrent and excurrent samples within each collection by Mann-Whitney *U*-tests to look for significant differences in densities between the reef ends. Second, I compared mean densities between incurrent and excurrent samples of each collection, and tested for incurrent-excurrent differences in these means among the eight collections with Wilcoxon's signed-ranks tests; thus, each collection was a paired (incurrent versus excurrent) observation.

Foraging Experiments

To see if blacksmith near the incurrent end consume more prey, I compared gut contents of fish that foraged near the incurrent kelp margin and excurrent shelter sites. I did not compare free-living adults because they were relatively rare near the excurrent end and their major activity might not have been foraging. Instead, I placed individuals in cages located at both ends of the reef. Cages were constructed of a 1 × 1 × 1 m

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

wooden frame covered with galvanized chicken wire, which allowed fairly free passage of water through the enclosure. For experiments using larger fish (>125 mm SL, standard length) the mesh measured 2.5 × 3.7 cm; mesh size was halved to 1.3 × 1.9 cm when smaller fish were used. Seine floats were attached to the top of the cages to make them positively buoyant, and the cages were suspended in midwater at a depth of 5 m by a length of rope anchored to the substratum. The cages were located in the same areas on the reef from which plankton were sampled. One cage was placed at the eastern margin of the kelp bed, 60 m east of the reef. The other was placed over the reef top, 50 m from the extreme west end of the reef (Figure 1). When half of the experiments were completed, the cages were translocated.

Blacksmith were captured while in shelters with the anesthetic quinaldine, or while attracted to chum stations (broken sea urchins). Fish were placed in holding tanks on the boat and haphazardly assigned to a cage. One to five fish were captured for each cage. Before each experiment, the cages were scrubbed with a brush to remove encrusting organisms. When fish were placed in the cage, they swam to the bottom; by the next day, they had usually gathered in the middle. At night, the fish nestled in the bottom corners of the cage.

Each experiment lasted 7-10 d. Preliminary experiments indicated that at least 5 d were required before caged fish began to feed. Fish were removed from cages in the midafternoon and fixed in buffered Formalin. On three occasions, I speared free-living fish in the vicinity of the incurrent cage at the same time that caged fish were removed, to see if caging affected the fish's diet. Since smaller blacksmith do not undergo large-scale movements and are abundant throughout the reef, I also compared gut contents of free-living juveniles speared at the incurrent and excurrent ends. For all collections, blacksmith at the incurrent end were removed first; those at the excurrent end within an hour later. Thus, positive differences in gut fullness between incurrent and excurrent fish are conservative because excurrent fish were able to forage for a longer period of time.

In the laboratory, fish were measured for standard length, blotted weight, and displaced volume. The gut was removed and divided into stomach and intestine. The contents of each were measured for displaced volume, then examined under a dissecting microscope and identified into broad taxonomic categories. Finally, contents were washed onto a preweighed filter and dried at 60° C to a constant weight.

To standardize for differences in fish sizes, the volumes and weights of the gut contents were expressed as relative measures: 1) volumetric fullness as $(Vg/Vf) \times 10^3$, where Vg is the displaced volume (in milliliters) of the gut contents, and Vf is the displaced volume (in milliliters) of the intact fish; 2) gravimetric fullness as: $(Wg/Wf) \times 10^4$, where Wg and Wf represent weights (in grams) of the gut contents and intact fish. Finally, for each experiment, I scaled volumetric and gravimetric fullness from 1.0 for the largest value, down toward 0, then averaged the two scaled values to obtain an overall estimate of gut fullness. This enabled me to pool data among experiments to increase sample size.

RESULTS

Physical Measurements

I made 39 surveys between December 1975 and July 1977. However, since water visibility directly influenced the volume of water in which I counted fish, I excluded from further analysis those surveys when mean visibility was significantly greater at the incurrent end of the reef (t-tests; $P<0.05$) or when variances in visibility at the incurrent and excurrent ends were heterogeneous (F-tests, $P<0.05$). In the remaining 27 surveys, water flowed over the reef from the east in 23; on 4 occasions (twice in April 1976, once in August 1976, and once in January 1977), the current was reversed and flowed from the west. Mean monthly water visibility ranged from 4.5 m in March to 8.7 m in December. Visibility was slightly greater at the excurrent end of the reef. When the current flowed from the east, visibility averaged 7.1 m at the east end and 7.4 m at the west end; when the current reversed, visibility averaged 6.0 m and 5.1 m at the east and west ends.

Spot checks on the movements of small particles indicated that the net flow of water was roughly unidirectional over most of the reef; this general flow was confirmed on 2 d when pieces of kelp were followed as they drifted the length of the reef (Bailey[3]). Nonetheless, variances in velocity were significantly heterogeneous between reef ends for

[3]Thomas Bailey, Marine Science Institute, University of California, Santa Barbara, CA 93106, pers. commun. June 1977.

individual measurements (F-max test, $P<0.001$), and for mean velocities among all 27 surveys (variances were: 41.10 incurrent, 16.05 excurrent; $P<0.05$). These variations were presumably caused by local turbulence produced by kelp and rocky prominences.

Current velocities were consistently greater at the incurrent reef end. When water flowed from the east, mean incurrent and excurrent velocities were 11.0 cm/s and 4.6 cm/s (Wilcoxon's signed-ranks test, $P<0.001$). When currents were reversed, incurrent and excurrent velocities were 4.9 and 3.6 cm/s ($P>0.25$); these differences probably would be significant with a larger sample size.

Water temperatures at the surface and midwater averaged 15.6° and 15.3° C, and both ranged from 13° C in April to 20° C in October. Bottom temperatures showed a similar pattern, but averaged approximately 2° C lower. Temperatures taken in 21 surveys when the current flowed from the east did not differ significantly between reef ends at any of the three depths (t-tests for paired samples, $P>0.25$). I recorded temperatures on only two of the four surveys when currents flowed from the west. Surface and midwater temperatures both averaged around 15° C while bottom temperatures averaged 13° C. I could not detect differences in temperatures between reef ends.

Role of Water Currents

The patterns in water visibility simplified my analysis of the fish counts. I treated each of the 27 surveys as a pair of samples, one from the incurrent and the other from the excurrent reef end. Each member of a pair consisted of a total count of blacksmith from the eight transects taken at one end of the reef (Figure 1). Differences within each pair were then analyzed among surveys with one-tailed nonparametric tests, with the hypothesis that counts of blacksmith are greater at the incurrent reef end. The similarity in water visibility between reef ends automatically standardized the counts for the volume of water that was sampled. Actually, the test of the hypothesis was conservative because visibility (hence the volume of water sampled) was significantly lower at the incurrent end in 6 of 27 surveys. I also calculated for each survey the proportion of blacksmith counted at each end of the reef. Proportions were arc sine transformed for computation of 95% confidence intervals (CI). I checked the precision of my surveys on two occasions by having another diver swim abreast of me and count blacksmith independently. Our total counts of adult blacksmith were similar: 103 (RNB) versus 112 (partner), and 254 (RNB) versus 273 (partner). Moreover, the surveys seemed to confirm our subjective impressions on the relative abundance of adult blacksmith and other fishes in the midwater.

Blacksmith were the most abundant fish in the midwater and were recorded on every survey. Other abundant fishes in the midwater were kelp bass, *Paralabrax clathratus*, and señorita, *Oxyjulis californica* (Table 1).

Adult blacksmith invariably aggregated at the incurrent end (Table 2). In each of the 27 surveys, more adults were counted at the incurrent than at the excurrent end (Wilcoxon's signed-ranks test, $P<0.001$). Doubling the length of transects had little effect on the counts of adults at the excurrent end, but resulted in a 3- to 4-fold increase in counts of adults at the incurrent end. This was because large numbers of adults gathered farther upcurrent, beyond the area covered in the short transects. The average proportion of adults at the east end of the reef was 0.99 (95% CI = 0.92-1.0) when it was the incurrent end, and 0.09 (95% CI = 0-0.32) when it was the excurrent end.

Adults respond quickly to changes in current direction. On one occasion around midday, the current reversed during a survey and the adults

TABLE 1.—Relative abundance (percentage of total individuals) and frequency of occurrence (percent of total surveys) of fishes counted in midwater transects at Naples Reef, southern California. Species are listed in order of decreasing abundance.

Species	Percentage of total individuals	Frequency (%)
Chromis punctipinnis	41.58	100.0
Paralabrax clathratus	22.04	100.0
Oxyjulis californica	9.47	81.5
Medialuna californiensis	9.00	92.6
Sebastes mystinus	8.62	55.6
Atherinops affinis	2.70	22.2
Trachurus symmetricus	1.82	25.9
Phanerodon furcatus	1.68	33.3
Sebastes serranoides	0.64	66.7
Brachyistius frenatus	0.59	33.3
Embiotoca jacksoni	0.42	33.3
Phanerodon atripes	0.39	18.5
Seriola dorsalis	0.29	11.1
Rhacochilus toxotes	0.21	18.5
Sebastes atrovirens	0.20	25.9
Embiotoca lateralis	0.20	3.7
Damalichthys vacca	0.05	22.2
Heterostichus rostratus	0.04	14.8
Girella nigricans	0.03	3.7
Mola mola	0.03	11.1
Torpedo californica	0.01	7.4
Sarda chilensis	0.01	3.7
Total no. of individuals	7,767	
Total no. of surveys	27	

TABLE 2.—Number of blacksmith per survey, average (median), in midwater surveys at the east and west ends of Naples Reef, southern California. Freq. = frequency of occurrence (percent of surveys). Short transects total 480 m; long total 960 m.

			Adults				Halfgrowns				Juveniles			
Current direction	Length of transects	No. surveys	Freq. (%)	East		West	Freq. (%)	East		West	Freq. (%)	East		West
East to west	short	16	100.0	44.2	(32.5)	0.6 (0.1)	31.3	0.9	(0.2)	0.3 (0.2)	12.5	1.9	(1.0)	10.9 (3.4)
	long	7	100.0	162.3	(171.0)	0.6 (0.4)	85.7	39.1	(18.0)	5.4 (1.6)	71.4	6.7	(3.0)	123.9 (198.0)
West to east	short	3	100.0	6.0	(8.0)	28.3 (25.0)	66.7	0.0	(0.0)	2.3 (1.0)	0.0	0	(0)	0 (0)
	long	1	100.0	3	(3)	84 (84)	100.0	3	(3)	3 (3)	100.0	30	(30)	30 (30)

TABLE 3.—Abundance of zooplankton at the east and west ends of Naples Reef, southern California. For each collection, differences in abundance between ends of the reef were tested with a Mann-Whitney *U*-test.

		Numbers Average no./m^3 ± 95% CI				Biomass Average mg/m^3 ± 95% CI			
Direction of current flow	Date 1977	No. samples	East	No. samples	West	No. samples	East	No. samples	West
East to west	19 Aug.	6	1,302.2±101.3*	5	485.0±260.7	6	34.8±3.1*	5	14.0±4.7
	29 Aug.	10	1,589.2±265.3ns	10	1,467.5±590.4	10	19.8±2.3ns	10	19.7±3.6
	15 Sept.	10	3,301.0±375.9*	10	2,809.4±214.7	10	48.1±4.3**	10	37.2±3.6
	21 Sept.	10	2,585.2±423.9**	10	1,095.8±278.5	10	32.0±3.4**	10	19.8±4.3
	29 Sept.	10	2,849.8±407.2ns	7	2,272.2±582.1	10	67.6±7.7*	7	53.0±6.6
	20 Oct.	10	3,277.5±427.5**	10	1,573.5±289.1	10	43.2±4.8**	10	28.5±2.9
West to east	7 Sept.	10	1,983.2±323.2**	10	3,184.3±253.8	10	41.7±6.3**	10	54.7±3.6
	11 Oct.	10	3,062.2±737.0**	10	5,314.2±539.9	10	44.3±9.3*	10	57.9±7.2

*$P \leq 0.05$; **$P \leq 0.01$; ns, not significant.

quickly migrated to the opposite end of the reef. I began the survey by counting fish at the west end. The current was flowing from the east and I did not count any adult blacksmith, although visibility averaged 12.2 m. I then started the survey at the east end and counted 81 adults, when the currents shifted and flowed from the west. While swimming the transects, I saw small schools of adults (5-15 individuals) moving toward the west (now incurrent) end. I returned to the boat and followed adults as they swam toward the west end, where I repeated the transects. Even though water visibility dropped to 5.0 m, I counted 43 adults over the area where, 2 h earlier, I had counted none.

The movements of halfgrown blacksmith were less clear. Counts were generally higher at the east end when the current came from the east (Table 2; Wilcoxon's signed-ranks test: short surveys, $P = 0.14$; long surveys, $P = 0.06$; short and long combined, $P = 0.05$). However, the pattern was inconsistent, and counts were actually greater at the west end in 3 of the 11 surveys in which halfgrown fish were sighted. The proportion of halfgrown fish at the east end averaged 0.90 (95% CI = 0.38-1.0). A similar inconsistency occurred when the current flowed from the west. All halfgrown fish counted were at the west end on the two short surveys in which they were seen, but the three individuals counted in the long survey were at the east end.

Juvenile blacksmith did not gather at the incurrent end. When the current flowed from the east, all juveniles were at the west end of the reef in the two short surveys in which they were seen and in the five long surveys (Table 2; Wilcoxon's signed-ranks test; long surveys, $P < 0.05$). The proportion of juveniles at the east end averaged only 0.03 (95% CI = 0-0.18). When the current flowed from the west, juveniles were not seen in the short surveys, and were equally abundant at both ends of the reef on the one long survey. However, these data do not accurately describe the response of juveniles to water currents. Observations along the bottom indicate that, regardless of the current direction, many juveniles occurred throughout the reef in stationary aggregations that form around shallow rocky prominences. The large number of juveniles counted at the west end reflected the location of the transects on the reef: almost 87% of the juveniles counted in the midwater surveys were seen in the two transects at the west end, which were the only transects over the shallowest part of the reef (Figure 1).

Zooplankton Densities

I took eight collections of zooplankton from mid-August to mid-October 1977 (Table 3). In six of the collections, the current flowed from the east; in the other two the current was reversed and flowed from the west.

Even though the counts of plankton were standardized to densities, I attempted to sample the same volume of water in each tow to make it equally likely that relatively rare items would be collected at both ends. In seven of eight collections, volumes of water sampled did not differ significantly between reef ends (t-tests, $P>0.10$); in the last collection a significantly greater volume of water was sampled at the west end of the reef ($P<0.01$). The average length of the tows was 57.1 m, which corresponds to a filtered volume of 11.2 m^3.

Small copepods (<4 mm carapace length) and cladocerans were the most abundant items in the samples, averaging 1,259/m^3 and 836/m^3. Small copepods dominated in 93 samples while cladocerans dominated in the remaining 55 samples. Most of the copepods were calanoids, although cyclopoids were also present. The majority of cladocerans appeared to be *Evadne* sp., but *Penilia* sp. occasionally dominated. Larvaceans ranked third in abundance, averaging 119.6/m^3.

Densities of zooplankton differed markedly between the incurrent and excurrent sample sites at Naples Reef. For each collection, mean number and dry weight of plankton pooled in excurrent samples were lower than those in incurrent samples, regardless of the current direction. Differences in counts were significant in six of the eight individual collections (Table 3), and for all eight collections tested together (Wilcoxon's signed-ranks test, $P<0.005$). Estimates of dry weights followed a similar pattern (Table 3).

The trend of a decreased abundance near the excurrent end was shared among many of the zooplankton groups (Table 4). Cladocerans, larvaceans, and bryozoan larvae were significantly less abundant at the excurrent end in seven of eight collections. Other groups were less abundant near the excurrent end in some collections but not in others. For example, densities of small copepods were significantly lower in excurrent samples in six collections, but were higher in another collection (Table 4). Overall, mean densities of 7 of the 15 plankton groups were significantly lower near the excurrent end. Cladocerans, small copepods, and larvaceans showed the greatest decrease near the excurrent end, while polychaetes and nauplii averaged slightly greater there.

Foraging Experiments

I attempted eight experiments between late July and mid-December 1977; three were deleted because several fish died in the cages. The following analysis is based on the 27 of 31 fish in the remaining five experiments that had food in their guts and showed no signs of injury. The first four experiments used larger individuals (117-214 mm SL); the last experiment used smaller fish (88-117 mm SL). For each experiment, there were only

TABLE 4.—Zooplankton densities near the incurrent and excurrent ends of Naples Reef, southern California. Densities are averaged among means of the eight collection days. Columns to the right indicate number of collections during which plankton densities at the incurrent end were greater, less than, or equal to those near the excurrent end (Mann-Whitney U-tests, two tailed; $P\leq0.05$). Symbols next to incurrent densities indicate P values from a one-tailed Wilcoxon's signed-ranks test for incurrent and excurrent differences in density among all collections combined. Plankton groups are listed in order of decreasing differences in densities between incurrent and excurrent ends of the reef.

Plankton group	Average number per m^3		Number of collections		
	Incurrent	Excurrent	Incurrent < excurrent	Incurrent > excurrent	Incurrent = excurrent
Cladocerans	1,097.2*	575.7	7	0	1
Small copepods	1,402.3ns	1,114.8	6	1	1
Larvaceans	178.7**	60.4	7	0	1
Echinoderm larvae	54.6ns	15.7	3	0	[1]2
Doliolids	41.8**	9.7	5	0	3
Chaetognaths	32.1*	16.9	6	0	2
Medusae	39.8**	25.0	5	0	3
Large copepods	22.8*	9.7	3	1	[1]3
Bryozoan larvae	15.5**	4.3	7	0	[1]0
Fish larvae	3.4ns	1.3	2	1	5
Decapod larvae	3.3ns	2.0	1	0	[1]3
Zoea	5.0ns	4.4	0	0	[1]5
Ostracods	0.3—	0.2	0	0	[1]1
Nauplii	1.0ns	1.2	0	0	[1]2
Polychaetes	0.9ns	1.4	0	0	[1]3

*$P\leq0.05$; **$P\leq0.005$; ns, not significant; — insufficient data;
[1] Not present in all eight collections.

minor size differences between fish in incurrent and excurrent cages (Table 5). Also, when data were pooled among experiments to increase sample size, neither length, weight, nor volume of fish differed significantly between cages (t-tests, $P>0.75$).

Gut fullness was greater for fish in the incurrent cage (Table 5). Average fullness for 13 incurrent

TABLE 5.—Diets of blacksmith in five cage experiments at the incurrent and near the excurrent ends of Naples Reef, southern California. Only individuals with food in their guts were included in the analyses. Fullness is defined in the text.

	Experiment dates, 1977									
	25 July-1 Aug.		3-12 Aug.		15-22 Aug.		9-19 Sept.		11-18 Oct.	
Item	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent
No. fish: with food, empty	4,0	5,0	3,0	2,1	1,1	1,1	1,1	2,0	4,0	4,0
SL (mm): $\bar{x}$	157.8	165.0	182.7	188.5	175	150	123	121.7	100.5	95.8
Range	145-179	145-187	167-195	161-214				117-129	90-117	88-117
Fullness: $\bar{x}$	0.70	0.30	0.67	0.06	1.0	0.36	1.0	0.47	0.57	0.18
Range	0.37-0.90	0.12-0.54	0.35-1.00	0.04-0.09				0.12-0.82	0.29-1.00	0.05-0.32
Food items	Average number per fish									
Larvaceans	981.3	77.5	148.3		153		452	201.5	482.3	370.3
Large copepods			8.0		67		172	2.5	70.3	2.3
Small copepods	82.3	186.8	12.7		57	20	148	62.0	211.0	156.8
Cladocerans	26.0	20.4						1.0	17.8	29.0
Chaetognaths			6.7					0.5	2.3	0.8
Decapod larvae		0.5						1.0	10.3	0.5
Polychaetes			0.7		10		23	1.5	1.0	3.0
Fish larvae		0.5								
Obelia sp.		3.5		7.5		3				
Total items	1,089.6	289.2	176.4	7.5	287	23	795	270.0	795.0	562.7

TABLE 6.—Diets of free-living and caged blacksmith at the incurrent end of Naples Reef, southern California. Fullness is defined in the text.

	Collection date, 1977					
	29 Sept.		18 Oct.		6 Dec.	
Item	Caged	Free	Caged	Free	Caged	Free
No. fish: with food, empty	3,0	5,0	4,0	5,0	3,1	4,0
SL (mm): Mean	113.7	114.8	100.5	112.2	91.3	100.3
Range	110-118	100-121	90-117	94-127	86-98	91-107
Fullness: Mean	0.34	0.73	0.32	0.69	0.81	0.46
Range	0.30-0.39	0.48-1.00	0.14-0.58	0.41-1.00	0.78-1.00	0.32-0.59
Food items	Average number per fish					
Larvaceans	200.3	1,904.6	482.3	805.4	561.3	865.8
Large copepods	134.0	302.2	70.3	563.6	952.7	267.0
Small copepods	102.0	321.2	211.0	397.6	295.3	615.3
Cladocerans	1.3	150.4	17.8	26.0	14.3	28.8
Chaetognaths	1.3	34.8	2.3	24.6	4.3	13.0
Decapods	2.7	10.2	10.3	27.8	5.3	2.3
Polychaetes	1.7	20.0	1.0	5.8	1.0	2.0
Total items	444.3	2,743.4	795.0	1,850.8	1,834.2	1,794.2

TABLE 7.—Diets of free-living juvenile blacksmith collected near the incurrent and excurrent ends of Naples Reef, southern California. Fullness is defined in the text.

	Collection date, 1977					
	29 Sept.		18 Oct.		20 Mar.	
Item	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent
No. fish: with food, empty	5,0	5,0	5,0	4,0	11,0	11,0
SL (mm): Mean	114.8	111.2	112.2	101.5	118.2	105.7
Range	100-121	85-117	94-127	85-116	101-122	98-114
Fullness: Mean	0.73	0.40	0.69	0.26	0.72	0.51
Range	0.48-1.00	0.04-0.61	0.41-1.00	0.02-0.83	0.62-0.93	0.02-0.81
Food items	Average number per fish					
Larvaceans	1,904.6	1,084.2	805.4	339.5	Not analyzed	
Large copepods	302.2	107.8	563.6	18.0		
Small copepods	321.2	292.8	397.6	313.3		
Cladocerans	150.4	207.2	26.0	34.5		
Chaetognaths	34.8	6.6	24.6	2.8		
Decapod larvae	10.2	4.6	27.8	8.0		
Polychaetes	20.0	8.6	5.8	1.3		
Total items	2,743.4	1,711.8	1,850.8	717.4		

fish, 0.70, was significantly greater than that for the 14 excurrent fish, 0.20 (Mann-Whitney *U*-test, $P<0.001$).

Nine categories of food items were identified from gut contents of caged blacksmith (Table 5). Larvaceans and copepods predominated, while other groups were usually rare or absent. All items were typically planktonic except for the sessile stage of the hydrozoan, *Obelia* sp., which quickly colonized cages even though they were scrubbed before each experiment. *Obelia* sp. occurred in gut contents as small branches (<5 mm long), and each was counted as one individual. Eliminating *Obelia* sp. would decrease gut fullness for excurrent fish even more (Table 5). Dietary variation between cages included differences in relative abundances of larvaceans and copepods, and additions of rare items in the excurrent cages. In the incurrent cage, larvaceans were the most abundant food items in all experiments, but in the excurrent cage, they were most abundant in only two experiments. When present, large copepods (>4 mm) were found mostly in incurrent-caged fish. Though relatively few in numbers, the size of these copepods (some nearly 10 mm long) probably made them nutritionally important. That excurrent fish ate *Obelia* sp. during three experiments is difficult to explain. Tufts of *Obelia* sp. may have been more abundant in the excurrent cages, because the excurrent cages appeared to foul at a faster rate. Sessile hydroids are not a normal food of blacksmith (Hobson and Chess 1976).

Caging altered the blacksmith diets, but the effects were variable. In two of three collections, free fish had generally consumed more food than caged fish (Table 6). Seven categories of food items were identified in the guts of caged and free fish. As before, larvaceans and copepods were by far the most abundant. Cladocerans were abundant in a few individuals, but chaetognaths, decapod larvae, and polychaetes were uncommon. Free fish ate mostly larvaceans in all of the collections, but caged fish were inconsistent. In one collection, caged fish ate mostly large copepods, but in the other two, they ate mostly larvaceans.

Free-living juveniles at the incurrent end ate more food than those at the excurrent end (Table 7). Pooled among collections, gut fullness differed significantly between reef ends (Mann-Whitney *U*-test, $P<0.05$). Nonetheless, dietary composition of all free-living juveniles was similar. Larvaceans always made up the most abundant item, with copepods and cladocerans also common. Numbers of small copepods were slightly less in excurrent fish, but the difference was not nearly so great as for larvaceans or large copepods. Numbers of cladocerans were greater in excurrent fish.

DISCUSSION

Blacksmith Distribution Patterns

Adults

The midwater surveys indicate that large numbers of adult blacksmith (>150 mm TL) swim to the incurrent end of Naples Reef. Under the usual current pattern of flow from the east, almost all adults recorded were at the east end; when currents reversed, adults were far more abundant at the west end. During one survey, adults were actually seen migrating to the opposite end as currents reversed. The only times I saw large numbers of adults dispersed throughout the reef occurred when currents were negligible. On another occasion at Toyon Bay, Santa Catalina Island (190 km southwest of Naples Reef), I saw a similar response of blacksmith to a current reversal.

Observations at night indicate that large numbers of blacksmith of all sizes take shelter in holes at the west (usually the excurrent) end of Naples Reef. Indeed, the density of sheltering blacksmith at the west end may exceed that at the east because higher rocky relief and more complex substratum at the west end provide more refuges. An investigation of the sheltering behavior of tagged blacksmith indicated that many individuals tend to return to the same shelter at night (Bray in prep.). Yet when the current flowed from the east, extensive searches throughout the entire reef during the day failed to reveal substantial numbers of adults anywhere but at the east end. During the present midwater surveys, I saw one of these tagged fish in a feeding aggregation at the extreme eastern margin of the kelp, almost 300 m away from the hole where it was tagged. This, and my observation that blacksmith swam the length of the reef when currents reversed, indicates that some adults must swim a considerable distance each day to gather at the incurrent end.

Juveniles

In contrast, juvenile blacksmith (<125 mm TL)

apparently do not congregate at the incurrent end. Although midwater counts were highest at the excurrent end, bottom observations indicate that juveniles occur abundantly throughout the reef. Some form large stationary aggregations about reef prominences while others are more dispersed, hovering within a few meters of the rocky substratum. Halfgrown fish are most abundant along the reef edge, between aggregations of adults and juveniles. To simplify the transects, I tallied blacksmith as though they were comprised of two major size classes, juveniles and adults; halfgrown fish made up but a small group of intermediate-sized individuals that allowed clearer distinction between these two classes. Actually, fish sizes ranged almost continuously from small juveniles to large adults. The degree of fish movements vary accordingly, from very short forays of newly settled juveniles to extensive migrations of large adults.

Foraging at Incurrent End of the Reef

Adults

In synthesizing day and night observations of fish residing on temperate and tropical Pacific reefs, Hobson (1973) concluded that when fish are active their dominant behavior is feeding, and when they are inactive they seek security either by schooling or by sheltering. Hobson (1972) states, "A suitable feeding location for any given species may or may not be near areas that offer it suitable security during its inactive period. Consequently, the major actions of these fishes characteristic of twilight relate to moving between feeding locations and shelter locations."

The most suitable foraging site for adult blacksmith, in terms of food availability, is likely at the incurrent end of the reef. The paired caging experiments indicated that the amount of zooplankton consumed by adults at the incurrent end was greater than the amount eaten by those over the reef near the excurrent end. Although the caging procedure itself did influence blacksmith foraging, I assume the effect was similar in both cages, so the differences in gut fullness reflected the relative availability of food at the reef ends.

There are at least two possible reasons for the greater food abundance at the incurrent end. First, plankton is probably replenished there at a faster rate. Measurements of current velocities indicated that water crossing the reef is slowed and deflected by rocky prominences and columns of giant kelp. When feeding in a current, blacksmith often position themselves in areas of slack water behind kelp while currents deliver food (Hobson and Chess 1976). On the other hand, fish in relatively calm water at the excurrent end may have to swim about, possibly farther from kelp or other shelter, to encounter food at a comparable rate. Hobson and Chess (1976) observed that feeding rates of blacksmith were greater in a moderate than a slack current.

Second, the density of zooplankton is greater at the incurrent end. Under the normal pattern of current flow with water coming from the east, zooplankton densities were consistently greater at the east end of the reef. Even more convincing, however, was the effect of current reversal; on these two occasions, zooplankton densities were significantly greater at the west end, with most of the differences attributable to decreased densities of cladocerans, small copepods, and larvaceans. I feel that the plankton samples provided a good measure of the abundance of the blacksmith's potential prey because the most abundant items in the plankton samples (copepods, cladocerans, and larvaceans) were also the major items found in the blacksmith guts. Also, I sampled in areas where blacksmith normally gather in the appropriate current conditions, and I was invariably surrounded by foraging adults while I collected plankton at the incurrent end. Although several investigators have discussed decreased densities of plankton in kelp beds (Limbaugh 1955; Quast 1968b; Miller and Geibel 1973; Feder et al. 1974), to my knowledge, this is the first quantitative documentation.

Juveniles

The incurrent end of the reef would seem to be the most suitable foraging site for juveniles—at least those that forage here consume more prey, as determined by the caging experiments and examinations of free-living individuals. But the surveys showed that juveniles fail to concentrate here, which indicates that other factors override the advantages of incurrent foraging.

Optimization models may be used to interpret foraging movements of planktivorous fishes (Reese 1978). While the benefits of movements usually involve energy gains, costs may include a variety of factors, such as competition, expendi-

tures of time and energy, and the threat of increased predation (e.g., Pyke et al. 1977). The differences in foraging movements between juvenile and adult blacksmith may indicate that although juveniles apparently benefit from foraging at the incurrent end, the cost of migrating to and maintaining station at the incurrent end might outweigh the benefit of greater food intake there. Smaller fish have lower cruising speeds and expend relatively more energy in swimming a given distance (Bainbridge 1958, 1960), so juveniles sheltering at the excurrent end may find it too costly to swim across the reef. Juveniles already at the incurrent end may remain near the bottom, because they find it too costly to maintain station in strong midwater currents. Hobson and Chess (1976) observed that in strong currents, blacksmith abandon open places for the lee of kelp plants. Similarly, when currents are strong over tropical reefs, diurnal planktivores approach the bottom (Hobson and Chess 1978).

Predation pressures may limit the movements of juveniles, which are vulnerable to many more predators than are the adults. Covich (1976:242) presented a simple graphic model that showed how predation can influence distances traveled by foragers if the threat of predation increased farther away from shelter; he stated, "Often the risk of predation to the forager and the distribution of resources are the major interacting variables that regulate consumer movement." In the tropics, juvenile fishes remain closer to reefs than adults, and at dusk when predation is most intense, smaller individuals seek shelter first (Hobson 1972, 1979). Many coral reef fish seek nearby shelter when predators approach (e.g., Hartline et al. 1972), and relocation experiments indicate that damselfishes released away from shelter are quickly eaten (Mariscal 1970; Nolan 1975). Similarly, the threat of predation might discourage juvenile blacksmith from aggregating in midwater at the incurrent end of Naples Reef. *Paralabrax clathratus* ranked second in abundance in my midwater surveys (Table 1), with larger individuals tending toward the incurrent end. Although these predators may exceed 700 mm TL (Miller and Lea 1972), they probably would have difficulty consuming large blacksmith. However, I have observed kelp bass >400 mm TL attacking juveniles, and gut analyses indicate they feed on a variety of small fishes, including juvenile blacksmith (Quast 1968d; Love and Ebeling 1978). Additional predators include other residential as well as open-water fishes, and marine birds and mammals.

Zooplankton Distribution Patterns

Residents Versus Nonresidents

Comparing differences in plankton densities across a reef has often been used to estimate the importance of plankton to the energetics of reef communities (e.g., Johannes and Gerber 1974). However, others have shown that inshore reefs also contain resident zooplankters with different habitat preferences. Many of these "demersal plankters" form a nocturnal component that either hides in the reef during the day and emerges at night (e.g., Alldredge and King 1977) or resides in deeper water during the day and moves into shallow areas at night (Hobson and Chess 1978, 1979). Thus, as several authors have pointed out (e.g., Alldredge and King 1977), differences in plankton densities across a reef might reflect the habitat preferences or patchiness of resident zooplankton, rather than the consumption of extrinsic zooplankton by fish or other reef residents.

It is doubtful that the incurrent-excurrent differences in plankton densities at Naples Reef resulted from sampling resident, demersal zooplankton. All samples were taken around midday in the water column away from reef or kelp substrata. At this time, most demersal forms hide in or near shelter or in deeper water (Alldredge and King 1977; Hobson and Chess 1976, 1978, 1979). Furthermore, typical reef residents—mysids, cumaceans, polychaetes, and decapods—were insignificant components in the plankton collections, while the groups that were consistently less abundant at the excurrent end—cladocerans and larvaceans—have not been reported as residential forms. However, it would be risky to conclude that the observed decline in zooplankton density across Naples Reef was entirely a consequence of predation by fishes and invertebrates of the kelp-bed community. I did not follow a specific parcel of water as it drifted across the reef; in fact, I sampled the excurrent end of the reef first in five of eight collections. Thus, at least some of the differences in plankton densities between the two ends may have been due to my sampling different patches of plankton. This would explain, e.g., the greater numbers of small copepods at the excurrent end in one collection (Table 4).

Impact of Blacksmith Foraging

Most of the food consumed by blacksmith comes from outside the reef community. Blacksmith diets, of course, depend on the composition of the plankton, but consist largely of larvaceans, cladocerans, and copepods. The same items dominate the diet of blacksmith off Santa Catalina Island (Hobson and Chess 1976). Some copepods may be members of the reef community (as discussed above), but the small calanoids in the blacksmith's diet are more likely a part of the drift plankton; residential forms probably would not occur during the day in the exposed, current-swept midwater areas of the incurrent end of the reef.

Too little is known about the total population and daily food consumption of blacksmith, and about the amount of plankton that passes over the reef, to accurately assess the effect of blacksmith foraging on incoming zooplankton. However, several lines of evidence indicate that blacksmith are major predators. The dominant items in their diets are those that showed the greatest decrease in abundance. Also, individual blacksmith consume a large amount of food each day. The guts of blacksmith are empty at dawn (Hobson and Chess 1976; Bray unpubl. data), so guts of individuals collected at dusk contain food that was consumed that day. The number of plankters in the stomach of 14 blacksmith (124-178 mm SL) that were speared as they sheltered at dusk averaged 1,455 items, 95% of which were larvaceans and small copepods. And these data underestimate the total number consumed. They exclude intestinal items, even though these largely unidentifiable remains weighed an average of 2.2 times the contents of the stomach, and they ignore items evacuated before dusk. Thus, considering that blacksmith composed over 42% of the 7,800 fish tallied, I conclude along with Limbaugh (1955) that they materially affect the plankton that is swept across southern California kelp beds.

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ESTIMATED INITIAL POPULATION SIZE OF THE BERING SEA STOCK OF BOWHEAD WHALE, *BALAENA MYSTICETUS*: AN ITERATIVE METHOD

JEFFREY M. BREIWICK,[1] EDWARD D. MITCHELL,[2] AND DOUGLAS G. CHAPMAN[3]

ABSTRACT

Initial stock sizes of bowhead whales were calculated iteratively, using an estimate of removals from the Bering Sea stock of bowheads, a range of assumed values for size of current stock, and assumed mortality and recruitment rates of $M = 0.04-0.08$ and $(r-M)_{max} = 0.01-0.05$. Estimates of initial stock size range between 14,000 and 26,000. At a kill level of 25 per annum, time to recover to 9,000 (50% of 18,000) is a minimum of 40 years if the present stock is approximately 2,700 bowheads. A theoretical model giving the risk of extinction is also discussed.

The International Whaling Commission has recently established quotas on the aboriginal take of the bowhead whale, *Balaena mysticetus*, in the Bering, Chukchi, and Beaufort Seas. This has led to much discussion of the status of the stock both now and in relation to its original size.

Bowhead whales are distributed throughout the Arctic in several presumably discrete stock units. Tomilin (1957) recognized four circumpolar stock units and Mitchell[4] identified five. Regardless of various interpretations, the Bering-Chukchi-Beaufort Sea stock has been regarded by all authors for many years as a discrete stock (Figure 1).

This stock winters in the Bering Sea, but during the spring it moves through the Bering Strait along the northwestern and northern coasts of Alaska at least as far as the Beaufort Sea. The Beaufort and Chukchi Seas are the main feeding areas. For convenience we will refer to this stock hereafter as the Bering Sea stock. This paper concentrates solely on this stock, for which commercial exploitation began in 1848, the date to which "initial" but not "unexploited" stock refers. Eskimo utilization of bowhead whales dates back many centuries, hence the Bering Sea stock was subject to human influence prior to 1848.

After 1848 the Bering Sea stock was rapidly depleted by heavy commercial exploitation—thus following a pattern that had been established earlier with respect to the Spitzbergen, Davis Strait, and Hudson Bay stocks and which also was to occur with the putative Okhotsk Sea stock (Mitchell footnote 4). Of all these depleted stocks, that of the Bering Sea is now the most abundant, and the only one from which removals of any consequence are occurring.

There are few satisfactory estimates of current population size for other bowhead whale stocks; estimates of the population sizes of all stocks at the onset of heavy commercial exploitation are even less reliable. Accordingly, we here present one approach to verify the order of magnitude of the early Bering Sea stock. We have also used some assumed estimates of the vital parameters in a simulation study of the expected time of recovery of this stock with catches at the present level.

The basis of the method is to start with an assumed current stock size and a recruitment rate, which is a function of stock size. The same form for the recruitment function is used throughout—a linear function decreasing from its maximum value at zero stock level to the natural mortality rate, M, at the initial stock level. Given current stock size, maximum net recruitment rate, mortality rate, and lag time between birth and age at recruitment into the fishery, the program starts with an estimated initial (1848) level. The pro-

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[4]Mitchell, E. D. 1977. Initial population size of bowhead whale (*Balaena mysticetus*) stocks: cumulative catch estimates. Int. Whal. Comm. Doc. SC/29/33, 112 p. The Red House, Station Road, Histon, Cambridge CB4 4NP, Engl.

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BEAUFORT SEA
CHUKCHI SEA
BERING SEA
BROOKS RANGE
CANADA
UNITED STATES
ARCTIC CIRCLE
NORTON SOUND
BERING STRAIT
Cross I.
Kaktovik (Barter I.)
Nuiqsut (Nuiqsut)
Pt. Barrow
Pt. Franklin
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Pt. Hope
Kivalina
Wales
Diomede
Savoonga
St. Lawrence I.
COLVILLE RIVER
Hotham Inlet
Kobuk R.
Noatak R.
Kotzebue
Selawik L.
Shishmaref
Deering
Candle
Buckland
Kiana
Ambler
Shungnak
Kobuk
Noorvik
Selawik
Kivalina
Noatak
Kotzebue

gram then calculates forward and adjusts the initial level until it yields the correct (i.e., assumed) current stock size. Current population estimates are based on sightings and therefore are presumably for the total population.

In order to reconstruct the 1848 level, it is necessary to have a record of the catch history since that time, together with a reasonable range of estimates of the other parameters noted, i.e., mortality rate, maximum net recruitment rate, and current population size. Estimated catches and other assumed parameter values are discussed below.

METHODS

Stock Size Analysis

Estimates of Initial Stock Size

Rice (1974), using data of Clark (1887), estimated a Bering Sea stock size of 4,000-5,000 animals during a peak harvest from 1868 to 1884. Mitchell (footnote 4) concluded that the period of peak catch was earlier and, after examining methods of extrapolating catch from production statistics (oil and baleen yield) and catch per vessel, constructed a catch history (1849-1976) based on these estimates or on known catch. Mitchell summed the cumulative catch for the peak decade (1851-60), applied a loss rate of 24%, and concluded that a minimum population of 11,647 bowheads existed in 1850. He then performed the same cumulative catch summation on what he termed the "residual stock," which had survived, and exploitation of which had resulted in another peak catch period in the 1880's-1890's.

In summing the two cumulative catch estimates of population size, Mitchell corrected the latter by subtracting from it an assumed net recruitment of 5% per year over the period between the peaks. He concluded that the initial stock must have comprised approximately 18,000 bowhead whales. The calculations discussed below are a refinement of this rough procedure and show that this estimate is not unreasonable.

Catch History

We have taken the best estimate of commercial catch for each year or the known catch when available, and applied the struck but lost (and assumed moribund) rates estimated by Mitchell (footnote 4). We have added to these commercial removals the known aboriginal catch (Maher and Wilimovsky 1963; Durham 1979) with some additions (Marquette 1976, see footnotes 5 and 6; Mitchell footnote 4) and adjusted by the struck but lost (and assumed moribund) rates estimated by Mitchell (footnote 4). These are summarized in Table 1 (cf. Mitchell's table 9) for the entire period 1848-1977 (see footnotes under Mitchell's table for discussion of extrapolations and modifications to these data).

Estimates of Current Stock Size

There have been few recent surveys or counts which give quantitative estimates of total population abundance. Counts, e.g., from ice edge sightings through the season, were made by Braham and Krogman,[7] who estimated the 1976 inshore migration from 25 April to 2 June to include 796 animals. Breiwick and Chapman[8] extrapolated these data to account for animals that migrated earlier than 25 April or later than 2 June and arrived at a total population of 1,227. However, a more complete and careful census was carried out in 1978, in which whales were counted in the nearshore lead as they passed Barrow, Alaska, between 15 April and 30 May. The estimate for this component of the population was 2,264 (Braham et al. 1979). Aerial surveys were conducted in offshore leads and no whales were observed. In the model below we assumed 1978 stock levels of 900, 1,500, 2,100, and 2,700 animals.

Vital Parameters

As stated above, we assume a recruitment model with appropriate parameter values. If natural mortality is assumed to be fixed and the net recruitment rate is a linear function of stock size, the

[5]Marquette, W. M. 1976. National Marine Fisheries Service field studies relating to the bowhead whale harvest in Alaska, 1975. Processed Rep., 31 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[6]Marquette, W. M. 1978. The 1976 catch of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos, with a review of the fishery 1973-1976, and a biological summary of the species. Processed Rep., 80 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[7]Braham, H. W., and B. D. Krogman. 1977. Population biology of the bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whales in the Bering, Chukchi and Beaufort Seas. Processed Rep., 29 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[8]Breiwick, J. M., and D. G. Chapman. 1977. Population analysis of the Alaska bowhead whale stock. Int. Whal. Comm. Doc. SC/SPC/13, 5 p. The Red House, Station Road, Histon, Cambridge CB4 4NP, Engl.

TABLE 1.—Estimated pelagic and Eskimo kill of bowhead whales from the Bering Sea stock.

	American pelagic fishery			Eskimo fishery					American pelagic fishery			Eskimo fishery			
Year	Catch	Loss rate[1]	Kill subtotal	Known kill[2]	Loss rate	Kill subtotal	Kill total	Year	Catch	Loss rate[1]	Kill subtotal	Known kill[2]	Loss rate	Kill subtotal	Kill total
1848	25	0.24	31	—	0.24	0	31	1913	15	0.24	19	5	0.56	8	27
1849	1,061	0.24	1,316	—	0.24	0	1,316	1914	—	—	—	4	0.56	6	6
1850	1,061	0.24	1,440	—	0.24	0	1,440	1915	—	—	—	3	0.56	5	5
1851	597	0.24	740	—	0.24	0	740	1916	—	—	—	14	0.56	22	22
1852	1,912	0.24	2,371	17	0.24	21	2,392	1917	—	—	—	15	0.56	23	23
1853	1,482	0.24	1,838	7	0.24	9	1,847	1918	—	—	—	9	0.56	14	14
1854	1,326	0.24	1,644	—	0.24	0	1,644	1919	—	—	—	4	0.56	6	6
1855	1,315	0.24	1,631	—	0.24	0	1,631	1920	—	—	—	14	0.56	22	22
1856	1,040	0.24	1,290	—	0.24	0	1,290	1921	—	—	—	2	0.56	3	3
1857	819	0.24	1,016	—	0.24	0	1,016	1922	—	—	—	17	0.56	27	27
1858	975	0.24	1,209	—	0.24	0	1,209	1923	—	—	—	3	0.56	5	5
1859	811	0.24	1,006	—	0.24	0	1,006	1924	—	—	—	29	0.56	45	45
1860	549	0.24	681	—	0.24	0	681	1925	—	—	—	32	0.56	50	50
1861	412	0.24	511	—	0.24	0	511	1926	—	—	—	18	0.56	28	28
1862	158	0.24	196	—	0.24	0	196	1927	—	—	—	7	0.56	11	11
1863	307	0.24	381	—	0.24	0	381	1928	—	—	—	11	0.56	17	17
1864	364	0.24	451	—	0.24	0	451	1929	—	—	—	16	0.56	25	25
1865	348	0.24	432	—	0.24	0	432	1930	—	—	—	7	0.56	11	11
1866	551	0.24	683	—	0.24	0	683	1931	—	—	—	18	0.56	28	28
1867	569	0.24	706	—	0.24	0	706	1932	—	—	—	7	0.56	11	11
1868	450	0.24	558	—	0.24	0	558	1933	—	—	—	5	0.56	8	8
1869	395	0.24	490	—	0.24	0	490	1934	—	—	—	4	0.56	6	6
1870	490	0.24	608	—	0.24	0	608	1935	—	—	—	6	0.56	9	9
1871	75	0.24	93	—	0.24	0	93	1936	—	—	—	10	0.56	16	16
1872	186	0.24	231	—	0.24	0	231	1937	—	—	—	15	0.56	23	23
1873	162	0.24	201	—	0.24	0	201	1938	—	—	—	11	0.56	17	17
1874	160	0.24	198	—	0.24	0	198	1939	—	—	—	8	0.56	12	12
1875	173	0.24	215	—	0.24	0	215	1940	—	—	—	12	0.56	19	19
1876	57	0.24	71	—	0.24	0	71	1941	—	—	—	23	0.56	36	36
1877	102	0.24	126	—	0.24	0	126	1942	—	—	—	11	0.56	17	17
1878	74	0.24	92	—	0.24	0	92	1943	—	—	—	7	0.56	11	11
1879	130	0.24	161	5	0.24	6	167	1944	—	—	—	2	0.56	3	3
1880	265	0.24	329	7	0.56	11	340	1945	—	—	—	12	0.56	19	19
1881	170	0.24	211	18	0.56	28	239	1946	—	—	—	12	0.56	19	19
1882	170	0.24	211	1	0.56	2	213	1947	—	—	—	11	0.56	17	17
1883	170	0.24	211	2	0.56	3	214	1948	—	—	—	5	0.56	8	8
1884	170	0.24	211	10	0.56	16	227	1949	—	—	—	6	0.56	9	9
1885	170	0.24	211	40	0.56	62	273	1950	—	—	—	9	0.56	14	14
1886	170	0.24	211	—	0.56	0	211	1951	—	—	—	14	0.56	22	22
1887	170	0.24	211	11	0.56	17	228	1952	—	—	—	4	0.56	6	6
1888	170	0.24	211	3	0.56	5	216	1953	—	—	—	23	0.56	36	36
1889	170	0.24	211	7	0.56	11	222	1954	—	—	—	4	0.56	6	6
1890	170	0.24	211	2	1.00	4	215	1955	—	—	—	23	0.56	36	36
1891	184	0.24	228	19	1.00	38	266	1956	—	—	—	7	0.56	11	11
1892	201	0.24	249	8	1.00	16	265	1957	—	—	—	3	0.56	5	5
1893	193	0.24	239		1.00	0	239	1958	—	—	—	2	0.56	3	3
1894	118	0.24	146	13	1.00	26	172	1959	—	—	—	1	0.56	2	2
1895	70	0.24	87	4	1.00	8	95	1960	—	—	—	19	0.56	30	30
1896	25	0.24	31	39	1.00	78	109	1961	—	—	—	10	0.56	16	16
1897	173	0.24	215	5	1.00	10	225	1962	—	—	—	12	0.56	19	19
1898	21	0.24	26	27	1.00	54	80	1963	—	—	—	10	0.56	16	16
1899	154	0.24	191		1.00	0	191	1964	—	—	—	16	0.56	25	25
1900	62	0.24	77	19	1.00	38	115	1965	—	—	—	7	0.56	11	11
1901	11	0.24	14	1	0.56	2	16	1966	—	—	—	15	0.56	23	23
1902	63	0.24	78	2	0.56	3	81	1967	—	—	—	4	0.56	6	6
1903	58	0.24	72	8	0.56	12	84	1968	—	—	—	17	0.56	27	27
1904	44	0.24	55	3	0.56	5	60	1969	—	—	—	19	0.56	30	30
1905	41	0.24	51	7	0.56	11	62	1970	—	—	—	25	0.56	39	39
1906	5	0.24	6	6	0.56	9	15	1971	—	—	—	24	0.48	36	36
1907	58	0.24	72	9	0.56	14	86	1972	—	—	—	38	0.48	56	56
1908	20	0.24	25	47	0.56	73	98	1973	—	—	—	37	0.48	55	55
1909	28	0.24	35	25	0.56	39	74	1974	—	—	—	20	0.48	30	30
1910	6	0.24	7	2	0.56	3	10	1975	—	—	—	15	0.48	22	22
1911	72	0.24	89	4	0.56	6	95	1976	—	—	—	48	0.48	71	71
1912	0	0.24	0	3	0.56	5	5	1977	—	—	—	32	—	111	[3]111
								Total	21,823		27,068	1,234		2,025	29,093

[1]100% moribund in those lost.
[2]Includes "commercial" shore-based landings in later years.
[3]29 killed + recovered; 3 killed + lost; 79 struck + lost.

resulting recruitment in numbers generates a logistic relationship. At initial stock levels the recruitment rate is assumed to be equal to the natural mortality rate (which includes a small amount of exploitation mortality at the pre-1848 level). As the stock is reduced, recruitment rate

increases proportionally, attaining its maximum level when the stock is near zero. However, it is also recognized that response in rate may occur with some lag and thus various lag periods are assumed.

In order to construct the model, various parameter estimates are needed. These are discussed below.

Net Recruitment Rate

Since information on the maximum net recruitment rate is lacking, a range of values (0.01-0.05) was used, based on analogy with other baleen whale stocks for which such data are available. For example, Allen (1972) showed calculated rates for the fin whale, *Balaenoptera physalus*, (as a proportion of exploited stock) to be mostly in the range 0.021-0.036. The Scientific Committee of the International Whaling Commission (International Whaling Commission 1978) calculated maximum gross recruitment rates for the sei whale, *B. borealis*, (as a proportion of exploited female stock) as 0.26 which implies a net recruitment rate of the exploited stock to be 0.06. If we express these rates as a proportion of the total stock, they are in the range of 0.01-0.05. (Furthermore, estimates of the 1848 stock level became unstable and did not converge if maximum net recruitment rates >0.05 were used in our iteration.)

Natural Mortality

Similarly, there is no information available on natural mortality in bowheads, and a range of values of 0.04-0.08 was used. These correspond to mortality estimates for other baleen species (Doi et al. 1967; International Whaling Commission 1971).

Lag Time

We have no data on the growth and age of this species, and there were no regulations in the fishery. Nor do we have any information on the lag that may occur between the reduction of stock density and response of the population through its presumed increase in recruitment. In a similar study carried out for porpoise stocks involved in the yellowfin tuna purse seine fishery (National Marine Fisheries Service[9]), lag periods of 1, 3, and 5 yr were used. Because the population response in larger animals might be delayed, we have arbitrarily tried four lag periods: 1, 3, 5, and 7 yr. As will be shown, this parameter has minor effect.

Model Development

The assumptions outlined above can be formulated in mathematical terms as follows. The recruitment model is

$$r_t = M + (1 - P_{t-\tau}/P_0)(r - M)_{\max}, \qquad (1)$$

where r_t = recruitment rate in season t
$P_{t-\tau}$ = population size at the beginning of season $t - \tau$ (τ = lag time assumed for population response)
P_0 = initial population size (start of 1848 season)
M = natural mortality rate
$(r - M)_{\max}$ = maximum net recruitment rate.

The extrapolation model also uses the (approximate) recursion formula (Allen 1966):

$$P_{t+1} = (P_t - C_t)e^{-M} + R_t \qquad (2)$$

where $R_t = r_t P_{t-\tau}$ is the gross recruitment between the beginning of season t and season $t + 1$, and C_t, P_t are catch in season t and population size at the beginning of season t. A further approximation made is that $e^{-M} = 1 - M$. Equation (2) provides a good approximation if the catching season is relatively short and natural mortality is low.

The iterative procedure consists of specifying a current stock level, natural mortality rate, maximum net recruitment rate, and iterating on P_0 in Equation (2). Thus

$$P_n = g(P_0, P_1, \ldots, P_{n-1}) \qquad (3)$$

where P_n is some current stock level. Due to the lag time involved in Equation (2), it is not practical to invert Equation (3) and solve for P_0 explicitly; hence the iterative solution of Equation (3) is obtained.

[9]National Marine Fisheries Service. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Adm. Rep. LJ-76-29, 54 p. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.

Risk Analysis

For any population there is a positive probability of its extinction, though for most populations this is negligibly small. However, the probability will increase as the population size is reduced, e.g., by direct or indirect action of man. Such direct action may be a harvest which is uncontrolled or one which is controlled by fixed rules that do not consider stochastic fluctuations in the environment.

Random fluctuations in the environment or population which cause increased mortality or reduced births can lead to extinction, particularly if the population is at a very low level. Moreover, the longer the population is maintained there, the greater the probability of extinction. Such risks of extinction have for a long time been the subject of study in population theory, but most such models are rather simple and include only statistical variation within the population but not externally imposed stresses. We now develop a model that expresses probabilities of extinction as a function of average population growth and variability of environmental stresses. In this model we assume that there is an average increment for each year but, superimposed on this, a variability of the environment which may result in the actual change being positive or negative. We define a stochastic process which is the sum of annual increments which are normally distributed with mean μ and variance σ^2, and with successive increments independent. It is known from the theory of stochastic processes (c.f., Cox and Miller 1965:58) that the probability of the process being absorbed by barriers at levels "a" above the initial value or "b" below the initial value are equal to

$$\frac{1 - \exp(2\,\mu\, b/\sigma^2)}{\exp(-2\,\mu\, a/\sigma^2) - \exp(2\mu b/\sigma^2)}$$

and

$$\frac{\exp(-2\,\mu\,/\sigma^2) - 1}{\exp(-2\,\mu\, a/\sigma^2) - \exp(2\,\mu\, b/\sigma^2)},$$

respectively. If b is set equal to the initial value, the second of these represents the probability of extinction. It is difficult to specify appropriate values for σ. For example, $\sigma = 100$ implies that with 95% probability the actual increase might vary from 200 above to 200 below the mean. Such variations are not unreasonable in the Arctic environment. We do not know if they are this large or not but catastrophic mortality due to ice conditions has been recorded (Sleptsov 1948, as cited by Tomilin 1957, in text but no citation given). We have assumed that stresses are independent events from year to year. To apply this we consider the female population which, in a total of 2,000, will number about 1,000. Extinction clearly occurs if this component falls to zero. We arbitrarily have assumed that if the female population reaches 2,000, the population is safe from extinction. If a larger "safe" upper limit is chosen, then the probabilities of extinction will be greater. It should be noted that the level of 2,000 females (or any other upper limit) is not an absorbing barrier in the sense that zero, the lower limit, is. However, to simplify the model, we have chosen a range within which it is reasonable to assume average growth is approximately constant—over a wider range the growth parameter must change. Because we have assumed constant μ (average increment), the probabilities of a population becoming extinct with 1,000 females are easily computed from the given formula for various levels of average annual increase and various levels of environmental stress as expressed by standard deviation.

RESULTS

Risk Analysis

The effect of the level of exploitation on the risk of extinction is shown in Table 2. A catch of 10 whales shifts the average increase downward by that amount; i.e., one moves one column to the left in the table. A continuing kill of 30 whales shifts the probabilities three columns to the left. Thus, if present net recruitment were 50 whales and the environmental perturbation were represented by $\sigma = 141.4$, the probability of extinction according to this model would be increased from 0.01 to 0.12 with a continuing 30 whale kill.

Initial Stock Size

It can be seen that the initial stock estimates are little affected by the estimates or assumptions of

TABLE 2.—Probabilities of extinction for stochastic process with normally distributed independent additive increments.

Stress variability σ	Average annual increase, μ					
	10	20	30	40	50	60
0.7	0.02	—	—	—	—	—
100	.12	0.02	0.002	—	—	—
141.4	.27	.12	.05	0.02	0.01	0.002
173.2	.34	.21	.12	.06	.03	.02

the current (1978) stock level given the same values of the other parameters $(r - M)_{max}$, M, and τ (Figure 2, Table 3). Table 4 shows the initial stock size estimates from Table 3 (1978 stock level of 2,700) reexpressed as deviations from row and column medians. The magnitude and direction of changes in the estimates as a function of the different parameter combinations indicate that in-

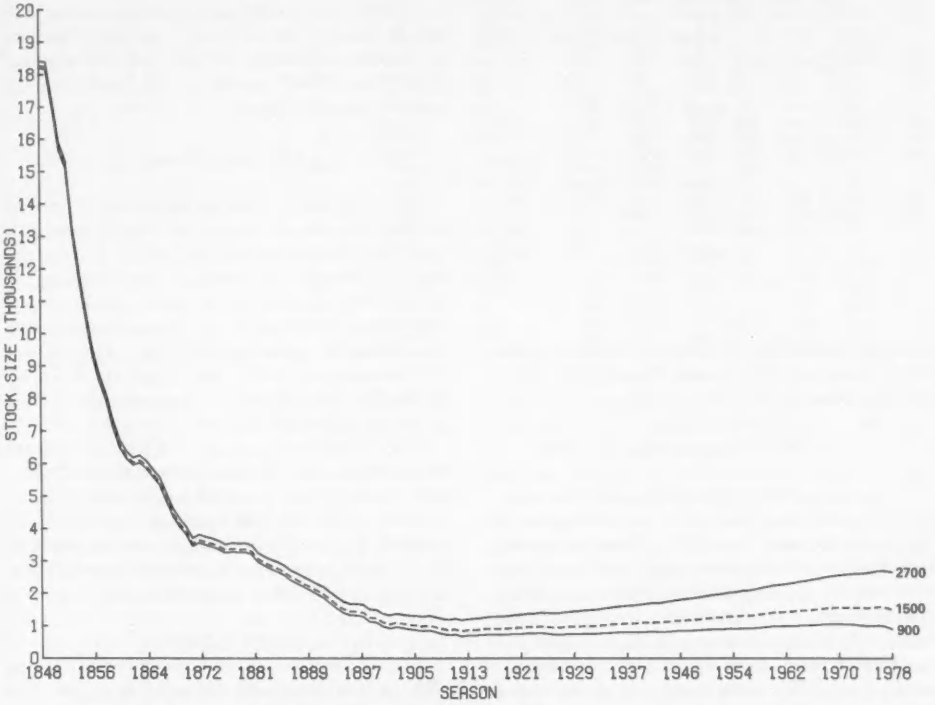

FIGURE 2.—Population back projections (where $M = 0.06$, Lag = 5 yr, $(r - M)_{max} = 0.03$) which would theoretically result in current stock sizes of 900, 1,500, and 2,700 bowhead whales according to the model (see text).

TABLE 3.—Results of iterative solution of Equation (3). Initial stock size estimates (in thousands) for various values of vital parameters (M, lag time, and maximum net recruitment rate) and 1978 stock level.

		1978 stock level of 900			1978 stock level of 1,500			1978 stock level of 2,100			1978 stock level of 2,700		
		$(r - M)_{max}$			$(r - M)_{max}$			$(r - M)_{max}$			$(r - M)_{max}$		
M	Lag time (yr)	0.01	0.03	0.05	0.01	0.03	0.05	0.01	0.03	0.05	0.01	0.03	0.05
0.04	1	25.67	21.95	19.64	25.91	21.98	19.64	26.15	22.02	19.65	26.40	22.05	19.65
.06		25.15	21.90	19.23	25.38	21.90	19.23	25.63	21.56	19.24	25.88	21.60	19.24
.08		24.62	21.41	18.82	24.86	21.44	18.82	25.10	21.10	18.83	25.35	21.14	18.83
.04	3	24.01	20.72	18.68	24.27	20.76	18.69	24.54	20.81	18.69	24.81	20.86	18.70
.06		22.77	19.69	17.78	23.04	19.74	17.79	23.31	19.80	17.80	23.60	19.85	17.81
.08		21.61	18.73	16.93	21.89	18.78	16.94	22.17	18.64	16.96	22.47	18.90	16.97
.04	5	22.56	19.63	17.83	22.84	19.69	17.84	23.13	19.76	17.86	23.43	19.82	17.87
.06		20.82	18.19	16.56	21.12	18.26	16.58	21.43	18.33	16.59	21.74	18.41	16.61
.08		19.29	16.90	15.42	19.60	16.98	15.44	19.92	17.11	15.57	20.25	17.16	15.49
.04	7	21.29	18.67	17.07	21.59	18.75	17.09	21.90	18.83	17.11	22.22	18.91	17.14
.06		19.21	16.92	15.52	19.53	17.02	15.55	19.86	17.11	15.57	20.20	17.21	15.61
.08		17.44	15.43	14.18	17.78	15.54	14.22	18.13	15.65	14.25	18.49	15.77	14.29

TABLE 4.—Reexpressed stock sizes of Table 3 (1978 stock level of 2,700).

		Row values minus medians				Column values minus medians		
	Lag	$(r - M)_{max}$				$(r - M)_{max}$		
M	time (yr)	0.01	0.03	0.05	Median	0.01	0.03	0.05
0.04	1	4.35	0.00	−2.40	22.05	0.52	0.45	0.41
.06		4.29	.00	−2.36	21.60	.00	.00	.00
.08		4.21	.00	−2.31	21.14	− .53	− .46	−0.41
					Median	25.88	21.60	19.24
.04	3	3.95	.00	−2.16	20.86	1.21	1.01	0.89
.06		3.75	.00	−2.04	19.85	.00	.00	.00
.08		3.57	.00	−1.93	18.90	−1.13	− .95	− .84
					Median	23.60	19.85	17.81
.04	5	3.61	.00	−1.95	19.82	1.69	1.41	1.26
.06		3.33	.00	−1.80	18.41	.00	.00	.00
.08		3.09	.00	−1.67	17.16	−1.49	−1.25	−1.12
					Median	21.74	18.41	16.61
.04	7	3.31	.00	−1.77	18.91	2.02	1.70	1.53
.06		2.99	.00	−1.60	17.21	.00	.00	.00
.08		2.72	.00	−1.48	15.77	−1.71	−1.44	−1.32
					Median	20.20	17.21	15.61

creasing values of M, lag time, and maximum net recruitment tend to decrease the estimate of initial stock size.

Vital Parameters

The natural mortality rate has somewhat less of an effect on initial stock estimates than does the maximum net recruitment rate. This can be seen from Table 4 where initial stock estimates have been reexpressed as deviations from row and column medians. As noted above, net recruitment rates >0.05 often did not result in convergence of the iterative procedure. In general, convergence occurred only if fractions of animals were allowed in Equation (2). If only integer numbers were used, it was virtually impossible to arrive at a prescribed stock level in 1978 from a given stock level. This is because the time series consists of over 100 yr, and rounding-off errors become critical if the convergence criterion is too stringent. We assumed convergence if the difference between two successive initial stock estimates was <0.1.

Maximum net recruitment rate and lag time are the most sensitive of the parameters we use in the model and natural mortality rate the least. We have used all combinations of the range of values of the parameters, although we recognize that certain combinations are likely to be unreasonable (for instance, a lag time of 1 yr with a maximum net recruitment rate of 0.01 is unlikely and therefore the initial stock size is unreasonable for these parameter values).

Bockstoce[10] examined a sample of maritime newspapers and logbooks of whaling voyages and estimated that 22,111 bowheads were killed by pelagic whalers in the "commercial" fishery between 1848 and 1915. Mitchell (footnote 4) estimated 27,714 whales killed in both the "commercial" and the "aboriginal" fisheries during this period. Initial stock size estimates using the data in Bockstoce (footnote 10) for 1848-1915 and our Table 1 for 1916-77 are about 15% lower than the results given in Table 3.

Recovery Times

Using the basic model of Equation (2) and assuming that the maximum net recruitment rate applies in the current season (assuming a population of 1,500 and 2,700 animals), the time required to recover to one-half of an initial stock level of 18,000 was calculated for various parameter values. These are presented in Table 5 as a ratio of time to recover to 9,000 with a constant kill (5, 10, 15, 20, 25, and 30 animals) compared with the time to recover without a kill.

If the current stock level were 1,500 animals and the maximum net recruitment rate was 0.05, M = 0.04, time lag 3 yr, the stock would take 58 yr to recover to a level of 9,000 with no kill vs. 75 yr with a kill of 30/year. These numbers are increased to 94 and 153 yr, when the maximum net recruitment rate is only 0.03 (other parameters unchanged).

DISCUSSION

We believe our model is useful but not fully adequate. We have reservations about the data used, limitations of the model, and aspects of the fishery that we did not have time or data to adequately address.

Limitations of the Data

The commercial catch data are based mainly on extrapolations of a consistent number of whales caught per ship. The statistics for the number of vessels operating in the bowhead fishery component of the North Pacific Ocean are also subject to

[10]Bockstoce, J. 1978. A preliminary estimate of the reduction of the western Arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry: 1848-1915. Report submitted to U.S. Marine Mammal Commission, Washington, D.C. Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA 22161, as PB-286-797.

TABLE 5.—Estimated recovery times for Bering Sea bowhead whale stock. Recovery time is that calculated with the parameters indicated, assuming zero kill. The relative increases in recovery time that occur with various levels of constant kill are tabulated in the last six columns.

Assumed current stock level	Lag time used in model	$(r - M)_{max}$	M	Recovery time (yr) to 9,000	Annual kill					
					5	10	15	20	25	30
1,500	3	0.01	0.04	273	1.22	1.63	[1]	—	—	—
			.08	302	1.21	1.58	—	—	—	—
		.03	.04	94	1.06	1.14	1.22	1.33	1.46	1.63
			.08	104	1.06	1.13	1.20	1.30	1.41	1.57
		.05	.04	58	1.05	1.09	1.12	1.17	1.22	1.29
			.08	64	1.03	1.06	1.11	1.16	1.20	1.27
	7	.01	.04	315	1.22	1.63	—	—	—	—
			.08	381	1.21	1.58	—	—	—	—
		.03	.04	110	1.06	1.14	1.22	1.33	1.45	1.63
			.08	131	1.06	1.13	1.21	1.31	1.43	1.59
		.05	.04	69	1.03	1.07	1.12	1.16	1.22	1.28
			.08	81	1.04	1.07	1.12	1.16	1.21	1.27
2,700	3	.01	.04	197	1.16	1.39	1.75	2.45	—	—
			.08	218	1.15	1.36	1.69	2.28	—	—
		.03	.04	68	1.04	1.09	1.15	1.22	1.29	1.38
			.08	74	1.05	1.09	1.16	1.22	1.28	1.36
		.05	.04	42	1.02	1.05	1.07	1.12	1.14	1.19
			.08	46	1.02	1.04	1.09	1.11	1.13	1.17
	7	.01	.04	226	1.16	1.39	1.74	2.45	—	—
			.08	274	1.15	1.36	1.69	2.28	—	—
		.03	.04	78	1.05	1.10	1.15	1.22	1.29	1.38
			.08	93	1.04	1.10	1.15	1.22	1.29	1.37
		.05	.04	48	1.04	1.06	1.08	1.13	1.17	1.21
			.08	57	1.04	1.05	1.09	1.12	1.16	1.19

[1]Stock goes to zero.

much interpretation (Mitchell footnote 4), but at least the extrapolations will approximate true trends.

The aboriginal catch data for some years may represent only the minimum landed catch. The pre-1960 aboriginal catch fluctuates from 0 to 47 (1908) per annum, where presently known. From 1978 back to 1854 there are many years for which no data were recorded or obtainable. Also, for many years for which data are available, the numbers given may not represent the true total landed catch. In our analysis, these unrecorded kills have implications only for the data from 1908 or 1912, near the end of the commercial pelagic fishery when the aboriginal catch begin to represent the majority of the total catch. However, during the much earlier period of high commercial catches, the aboriginal catch composed a small percentage of the total (5% or less of the pelagic catch at its highest). Thus any analysis of recovery patterns dependent upon the post-1900 data is entirely dependent upon the completeness of the aboriginal catch. Since few contemporary written records have been kept and continued library research yields new figures for given years, the aboriginal catch must be regarded as minimum and provisional.

Limitations of the Model

All models with published results previously used on whale populations have been applied to odontocetes, balaenopterids, or eschrichtiids, but not to balaenids. Because we are dealing with a separate zoological family (much older than the balaenopterids and apparently different in many behavioral features), caution should be used when applying balaenopterid vital parameter values, by analogy, to the balaenid model. No other reasonable estimates are available, however.

Although the model (Equation 2) used to estimate initial abundance is relatively simple, it does account for fishing and natural mortality and recruitment as a function of the time-lagged population size. It is quite possible, though, given the 130 yr we are considering, that the natural mortality rate has changed. Such a change, if it has occurred, probably would have had a relatively small effect on the initial stock estimates. We have also not considered the effect of a differential sex ratio in the large pelagic catches, which could have resulted in the 1912 population consisting of (in the worst possible cases) mostly males, mostly old females of low fertility, or young animals of either sex.

Although Figure 2 shows a minimum population size occurring around 1912, we have not calculated the minimum size the population might have declined to, for the following reasons: assumptions that the population was much smaller then (and has appreciably recovered) cannot be proven, and represent only one alternative explanation of the

history of the fishery and of the population since the early 1900's. For example, we do not know how the 1912 population was structured. If, as seems likely with high prices for baleen, selection mainly for large animals with long baleen occurred near the end of the fishery, then the remnant population might have comprised a large proportion of young animals. The 1977 population might represent a considerable proportion of this 1912 population, now old, and we would know little about net recruitment or failure thereof.

The most difficult parameter to estimate in any whale population is the recruitment rate. In the absence of better knowledge, we have used a simple linear model and specified a range of maximum net recruitment rates. Given that the recruitment rate function varies between some maximum value at stock level near zero and M at P_0, the shape of the curve has less effect than the value of $(r-M)_{max}$. During the early history of the fishery, catches exceeded recruitment, and during the last half-century the stock was at a relatively low level. Thus, the recruitment rate was close to its maximum and varied little. A further study could consider the effect of a dome-shaped recruitment curve.

Given our results, it appears likely that stock size between 1910 and 1978 was probably <10% of the initial stock level. According to most classical models used with baleen whale populations, the net recruitment should have been near its maximum for about the last 60 yr. Because the population does not appear to have grown substantially since then, either the recruitment rate has been low or the kills have been higher than currently estimated. It is also possible that the catches during the last half-century represent survivors of the then young animals.

Aspects of the Fishery

We may have to consider very low net recruitment rates because the changing nature of the fishery suggests that, as the worst case, the whalers efficiently decimated a structured population successively over its geographic range. The argument is as follows: females with calves migrate farther north (later, in the migration stream) and also inhabit ice fields. They might not have been as available to the early fishery, 1850-ca. 1870's, which used sailing vessels at the ice edge and which was mainly a midsummer to late season fishery. The greatest removals were during this time and for a short period. Subsequently, with the development of steam whaling, overwintering of the fleet became possible, and heavy fishing occurred in the ice fields at all times. The fishing season was effectively increased in length between the 1880's and 1910's. (Even if the population were not so structured by sex or age, the present spring and summer distribution is confined to a much smaller area compared with the data of Townsend (1935).)

Due to the unique geography, stratification, and timing of this fishery, the possibility exists that once the stock is fished to some low level, recruitment failure could occur and that net recruitment since about 1900 could indeed be as low as 0.01, the minimum figure used in our calculations.

Any subsequent analysis of annual catch and effort data (e.g., including number of vessels, etc.) should consider changing technology. The fishery changed radically from one of a sailing vessel-ice edge-early season fishery to a steam vessel-ice pack-nearly year round fishery. The best measure of change in effort between sailing and steam vessels to catch the same number of whales might be the monthly duration of the respective voyages.

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SPAWNING BIOMASS AND EARLY LIFE OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, IN THE NORTHERN SUBPOPULATION OFF OREGON AND WASHINGTON

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ABSTRACT

A major spawning center for the northern subpopulation of northern anchovy, *Engraulis mordax*, is documented off the Oregon-Washington coast beyond the continental shelf, based on collections of planktonic eggs in July 1975 and July 1976. Biomass estimates of northern anchovy in this spawning concentration ranged from 262,506 to 769,511 metric tons in 1975 and 144,654 to 1,005,263 metric tons in 1976, based on egg and larva surveys. Spawning biomass was estimated to be 800,000 metric tons in 1977, based on an acoustic survey of adults. The most probable biomass may be more than 100,000 but less than 1,000,000 metric tons. Potential yield estimates ranged from 86,792 to 633,316 metric tons, but realizable yields may be considerably lower if management strategies applied to northern anchovy in the central subpopulation are implemented for the northern subpopulation.

Spawning appears to be associated with waters of the Columbia River plume which may provide favorable conditions, in terms of stability and productivity, for survival of first feeding northern anchovy larvae. Evidence of larval transport south away from the spawning center leads to questions about return mechanisms to explain the occurrence of juveniles in Oregon bays and rivers later in the season. Additional spawning centers within the range of the northern subpopulation have not been documented although some evidence from the literature indicates another spawning center may occur in the Strait of Georgia, British Columbia, around the Fraser River plume.

Conditions related to spawning differ between the northern and central subpopulations. Off Oregon, spawning occurs from mid-June to mid-August, when current flow to the south is at a maximum, water temperatures are reaching maximum levels for the year, coastal upwelling is at a maximum, and day length is at or near maximum duration. Off California, peak spawning occurs from January through April when southward current flow is minimal, water temperatures are reaching minimal levels for the year, upwelling is minimal, and day length is at minimum duration. These factors are indicative of some degree of reproductive isolation as well as differing reproductive strategies between the two subpopulations.

The northern anchovy, *Engraulis mordax* Girard, is an abundant pelagic schooling fish that occurs along the west coast of North America from Cape San Lucas, Baja California, to the Queen Charlotte Islands, British Columbia (Miller and Lea 1972; Hart 1973). It is the object of an expanding fishery off central and southern California and Baja California where about 204,000 metric tons (t) were harvested in 1975, mainly for fish meal (Pacific Fishery Management Council[2]). In the northern part of its range it is utilized only to a small degree as bait by local fishermen although its potential as a harvestable resource has been suggested (Pruter 1966, 1972). Reports of dense schools off the Oregon and Washington coasts indicate northern anchovy biomass may be substantial (Pruter 1966, 1972). Estimates of an annual consumption of 28,000 t of northern anchovy by four species of marine birds off the Oregon coast (Wiens and Scott 1975) further indicates sizeable biomass.

In the absence of a fishery, biomass estimates are unavailable for northern anchovy north of California. We know that in the 1940's northern anchovy in ocean waters adjacent to the Columbia River supported a live bait fishery for albacore tuna (Pruter 1966, 1972). Reported commercial landings of northern anchovy in Washington in 1947-49 ranged from 20 to 182 t annually and were 28 and 76 t in Oregon in 1948 and 1953 (Pruter 1966). A small purse seine fishery for canning once existed around southern British Columbia where harvests ranged from 64 to 6,201 t annually between 1939 and 1947 (Roach and Harrison 1948; Pike 1951).

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[2]Pacific Fishery Management Council. 1978. Northern anchovy fishery management plan. U.S. Dep. Commer., NOAA Federal Register 43(141) Book 2:31651-31783.

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Because of the relatively unfished state of northern anchovy off Oregon and Washington, the lack of biomass estimates, and the potential for fishery development, this study was undertaken to define spawning centers and provide the first preliminary estimates of spawning biomass within such defined spawning centers by means of ichthyoplankton survey. Additional information on adult school distributions and another independent estimate of biomass were obtained by acoustic survey (Smith[3]). Ecological data on the early life of these northern occurring fish were also examined. Aspects of adult life history, particularly reproduction, are presented in a separate paper (Laroche and Richardson 1981).

THE NORTHERN SUBPOPULATION

Northern anchovy occurring north of Cape Mendicino, Calif., compose the northern subpopulation of *E. mordax*, one of three subpopulations (Figure 1) distinguished on the basis of meristic counts (McHugh 1951) and electrophoretic separation of blood serum protein (Vrooman and Paloma[4]). The central subpopulation occurs primarily off southern California and northern Baja California and the southern subpopulation is off central and southern Baja California. A separate subspecies, *E. mordax nanus*, has also been described from San Francisco Bay (Hubbs 1925).

Compared with the central and southern subpopulations, relatively little detailed information is available on spawning and early life history of northern anchovy in the northern subpopulation. Off California and Baja California spawning seasons and locations are well defined (e.g., Ahlstrom 1966, 1967; Baxter 1967; Kramer and Ahlstrom 1968), eggs and larvae have been illustrated (Bolin 1936; Ahlstrom 1956, 1965; Kramer and Ahlstrom 1968), and spawning biomass has been estimated on the basis of larva survey (e.g., Pacific Fishery Management Council footnote 2).

For the northern subpopulation, information on spawning and early life history had to be pieced together from a number of sources to provide the background for the present study. Based on monthly plankton collections of larvae off Oregon

FIGURE 1.—Geographic ranges (hatched) of the three subpopulations (northern, central, southern) of *Engraulis mordax* (modified from Smith and Lasker in press). Rectangular area outlined off Oregon and Washington shows ichthyoplankton survey grid boundaries for this study. Rectangular area outlined off California and Baja California shows approximate boundaries of the principal portion of the CalCOFI survey grid (after Kramer et al. 1972).

(Richardson 1973, see footnote 5; Richardson and Pearcy 1977) and maturity studies involving measurements of ova diameters from ovaries of fish collected off British Columbia (Pike 1951), the spawning season is short, lasting from about mid-June to mid-August. Based on available catch records (Williamson 1929 [in Pike 1951]; Pike 1951;

[3]P. E. Smith, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1978.

[4]Vrooman, A. M., and P. A. Paloma. 1975. Subpopulations of northern anchovy, *Engraulis mordax* Girard. NOAA NMFS Southwest Fish. Cent., Admin. Rep. No. LJ-75-62, 10 p.

[5]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay Oregon: abundance, distribution, and seasonality January 1971 to August 1972. Oreg. State Univ. Sea Grant Coll. Prog. Publ. No. ORESU-T-77-003, 73 p.

Parsons et al. 1970; Eldridge and Bryan 1972; Blackburn 1973; Richardson 1973, footnote 5, unpubl. data; Pearcy and Myers 1974; Laroche 1976; Misitano 1977; Richardson and Pearcy 1977; Waldvogel 1977; Robinson[6]; Cummings and Schwartz[7]; Forsberg et al.[8]) spawning locations have not been well defined and data are somewhat contradictory. Before the present study, running ripe adults had never been collected. Two nearly ripe females were taken in coastal waters around British Columbia; one ripening female was taken in Tillamook Bay in northern Oregon; and large numbers of ripening adults had been found in Humboldt Bay in northern California (Figure 1). Interestingly, the ripening fish in Humboldt Bay leave in June or July and return again in fall in a spent condition. Planktonic northern anchovy eggs had been reported only from certain inlets of Vancouver, British Columbia, in Puget Sound, Wash., off the Columbia River mouth, and in Yaquina Bay, Oreg. Small (<10 mm) planktonic larvae had been rarely taken in areas where ripening adults or planktonic eggs had been found. Small numbers of these larvae had been reported only from Yaquina Bay and Humboldt Bay. Large concentrations of small larvae had been reported only from ocean waters off Oregon. Larvae ≥10 mm had been taken in small numbers in the Strait of Georgia, British Columbia, inside the mouth of the Columbia River, in Yaquina Bay, and in Humboldt Bay. As with small larvae, large concentrations had been found only off the Oregon coast. Juveniles ≥35 mm had been taken in ocean waters off Oregon as well as in the Strait of Georgia, British Columbia; Puget Sound, Wash., inside the Columbia River mouth; in Tillamook Bay, Yaquina Bay, and Coos Bay, Oreg.; and in Humboldt Bay, Calif. Juveniles taken offshore were usually <50 mm while most of those in bays and sounds were >50 mm.

These data, and particularly the earlier study by Richardson (1973), indicated the possible existence of a spawning concentration of northern anchovy within the northern subpopulation located off the Oregon-Washington coast. Richardson suggested spawning might be associated with the Columbia River plume. The present study was designed to test that hypothesis and to estimate the biomass of spawning adults located therein.

METHODS

Field Procedures

Standard ichthyoplankton surveys (Smith and Richardson 1977) were conducted off the Oregon-Washington coast in the region outlined in Figure 1. This survey area was designed to border at least the inner bounds of the Columbia River plume. Cruises were conducted at the presumed time of peak spawning in mid-July: 10-18 July 1975 and 7-15 July 1976.

A grid of 70 stations along seven east-west transects (Figure 2) was sampled. Stations ex-

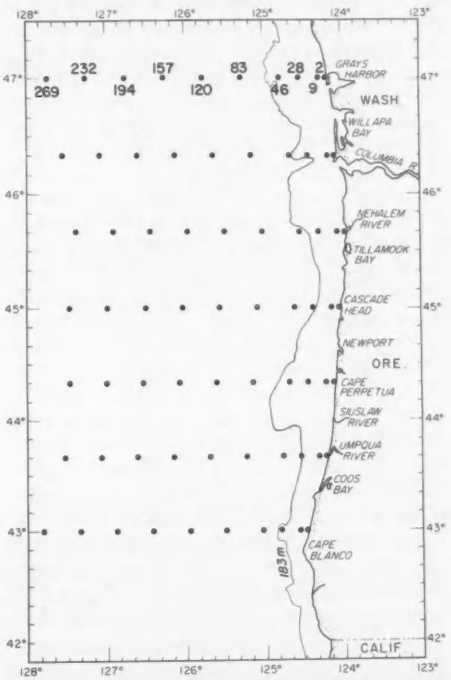

FIGURE 2.—Ichthyoplankton survey grid with 70 cm bongo net sampling stations occupied in July 1975 and July 1976 off Oregon and Washington. Numbers on upper transect represent kilometers from the coast and apply to all seven transects.

[6]Robinson, D. G. 1969. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4-6, 1967. Fish. Res. Board Can., Manuscr. Rep. Ser. No. 1012, 71 p.

[7]Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Fish. Comm., Res. Div., Coastal Rivers Invest. Inf. Rep. 70-11, 22 p.

[8]Forsberg, B. O., J. A. Johnson, and S. M. Klug. 1976. The identification, distribution, and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oreg. Dep. Fish Wildl., Res. Sect., Fed. Aid Prog. Rep.: Fish., Feb. 1974-June 1976, 117 p.

tended from 2 to 269 km offshore and covered a north-south distance of 450 km. Transects were 74 km apart and stations on a transect were 46 km apart except the most inshore stations which were closer together. The grid covered an area of 120,150 km².

Oblique 70 cm bongo net tows were made at each station from 150 m (or just above the bottom) to the surface. Vessel speed was 2-3 knots and retrieval speed was 20 m/min. The bongos were fitted with 0.333 and 0.571 mm mesh Nitex[9] nets, TSK flowmeters and a time-depth recorder. Stations were occupied when the ship arrived, day or night. Samples were preserved in 10% buffered Formalin.

Temperature, salinity, and chlorophyll were monitored at 3 m depth every 9 km along each transect using a flow-through fluorimeter system (AMINCO Fluro-colorimeter). At each bongo station a bathythermograph cast was made to 140 m depth (or 5 m above the bottom) and a surface bucket temperature was recorded. During the July 1976 cruise, surface drifters, consisting of a labelled plastic tag made buoyant with Styrofoam, were released to provide information on surface water movement. Fourteen drifters were dropped at each bongo station except on the southernmost transect (lat. 43°00′ N) where only 10 were released at the 120 km station and none at the 157, 194, 232, and 269 km stations.

Between 18 and 25 July 1977 an acoustic survey was conducted cooperatively by the National Marine Fisheries Service (NMFS) in the same area as the previous ichthyoplankton surveys (Smith[10]). The same seven transects plus an eighth transect to the south along lat. 42°20′ N were surveyed acoustically during daylight using the methods of Smith (1970). Distance covered on each line extended from the 91 m depth contour westward 167 km. In addition to the acoustic work, temperature and salinity at 3 m depth were monitored every 9 km using a flow-through salinograph, and expendable bathythermographs were cast every 9 km on every other transect. Following a day's sonar run, nighttime surface trawls were made with a 40 m modified Cobb pelagic trawl (Smith footnote 10) on the latter half of the sonar track in areas of biological aggregations identified and measured by sonar. Standard oblique 60 cm bongo tows (Smith and Richardson 1977) were made at each trawl station from 70 m to the surface. Samples were processed at sea using CalCOFI (California Cooperative Oceanic Fisheries Investigations) techniques (Kramer et al. 1972) except that the 0.333 mm mesh samples were preserved in ethyl alcohol for special studies (Methot[11]).

Laboratory Procedures

Plankton volumes for each 0.333 mm mesh bongo sample from the 1975 and 1976 cruises were determined by displacement (Kramer et al. 1972), and northern anchovy eggs and all fish larvae were sorted. Northern anchovy eggs were enumerated. Measurements of long and short axes of eggs were made on selected samples using an ocular micrometer in a stereomicroscope. Northern anchovy larvae were identified, enumerated, and measured in 0.5 mm size classes using a plastic rule beneath a glass slide. The 0.333 mm mesh bongo samples only from the 1977 cruise were processed by personnel from Scripps Institution of Oceanography and the NMFS Southwest Fisheries Center according to techniques described by Kramer et al. (1972). Numbers of eggs and larvae in each sample were standardized to the number under 10 m² sea surface (Smith and Richardson 1977):

$$C_i = 10\,(a_i^{-1} b_i^{-1} c_i d_i) \qquad (1)$$

where C_i = number of eggs or larvae beneath 10 m² sea surface at station i
a = mouth area of the bongo net used at station i in square meters
b = length of tow path in meters estimated from a calibrated flowmeter at station i
c = number of eggs or larvae in the ith sample
d = maximum depth of tow in meters.

Egg and Larva Census Estimates

Census estimates (i.e., estimates of the total number of northern anchovy eggs and larvae in

[9]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[10]Smith, P. E. 1977. Cruise report, R/V *David Starr Jordan*, 7705(111), Mordax North, Leg A, 13-27 July 1977. Rep. dated 5 December 1977. On file at National Marine Fisheries Service Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[11]R. D. Methot, Scripps Institution of Oceanography, Graduate Department, La Jolla, CA 92093, pers. commun. July 1977.

the area represented by the survey grid during each cruise in 1975 and 1976) were determined by two methods, the Sette and Ahlstrom Census and the Smith Census. The Sette and Ahlstrom Census was the polygon method of Sette and Ahlstrom (1948) in which the number of individuals under 10 m^2 sea surface at each station was weighted by the area represented by the station. These areas are polygons formed "by constructing perpendicular bisectors of lines drawn from the station to each of all surrounding stations" (Sette and Ahlstrom 1948). The census estimate is then:

$$C_k = 10 \sum_{i=1}^{n} A_s \, (a_i^{-1} b_i^{-1} c_i d_i) \qquad (2)$$

where C_k = estimate of abundance of eggs or larvae during cruise k
A_s = area of a polygon constructed of perpendicular bisectors of lines between station i and all adjacent stations
n = number of stations.

Polygon areas, determined by planimeter, ranged from 0.38 to 2.89×10^9 m^2 but were $>2.00 \times 10^9$ m^2 for all stations 46 km or more from the coast.

The Smith Census was the "regional census estimate" of Smith (1972):

$$C_{kr} = 10 \, A_r n^{-1} \sum_{i=1}^{n} (a_i^{-1} b_i^{-1} c_i d_i) \qquad (3)$$

where C_{kr} = estimate of abundance of eggs or larvae in region r during cruise k
A_r = area of region r in numbers of 10 m^2 areas (in my study,

$$10 \, A_r = \sum_{i=1}^{n} A_s = 148.81 \times 10^9 \text{ m}^2).$$

The Smith Census method can be less tedious than the Sette and Ahlstrom Census method if the area represented by the survey can be determined in a gross manner, i.e., without planimetry. Values of the Smith Census in my study were always lower than those of the Sette and Ahlstrom Census. The Smith Census was computed here primarily to allow for comparison with CalCOFI data (Smith 1972; Pacific Fisheries Management Council footnote 2).

Spawning Biomass Estimates

Four methods were used to estimate spawning biomass, three based on egg census estimates (Sette and Ahlstrom Egg Method, Simpson Egg Method, Saville Egg Method) and one based on larva census estimates (Smith Larva Method). The use of three egg methods generally follows the approach of Houde (1977) in estimating spawning biomass of round herring, *Etrumeus teres*. Because the shape of the egg production curve throughout the spawning season is unknown for northern anchovy, the use of these three egg methods takes into account the range of possibilities (discussed below) for comparative purposes.

All three egg methods ultimately use the same formula (Saville 1964) to estimate spawning biomass:

$$B = \frac{E_s}{KF} \qquad (4)$$

where B = biomass of spawning adults
E_s = total number of eggs spawned during a season, i.e., seasonal egg production. (This estimate varies according to the egg method used as described below.)
K = the proportion of spawning adults that are females. [In this paper the overall sex ratio of *E. mordax* is assumed to be 1:1 following Smith (1972) and Klingbiel (1978).]
F = mean fecundity, i.e., the number of eggs produced per gram of female per spawning season. [The mean fecundity of *E. mordax* in the northern subpopulation off Oregon is estimated to be 720 ova/g total weight female (Laroche and Richardson 1981).]

The number of eggs spawned in a season (E_s) was estimated by three methods, each using the two egg census estimates described above.

The Sette and Ahlstrom Egg Method of estimating seasonal egg production (E_s) follows the approach of Sette and Ahlstrom (1948).

$$E_s = \sum_{i=1}^{N} \frac{C_k D_i}{t_i} \quad \text{or} \quad \sum_{i=1}^{N} \frac{C_{kr} D_i}{t_i} \qquad (5)$$

where N = number of cruises in a season
D_i = number of days represented by cruise i. [Sette and Ahlstrom (1948) defined this to be the days included in the cruise plus one-half the days since the previous cruise and one-half the days to the next cruise; in this study only one cruise was made during the spawning season and the number of days represented by the cruise was taken to be the entire spawning season. Duration of the spawning season for *E. mordax* off the Oregon-Washington coast was estimated from monthly or bimonthly collections of larvae taken off Oregon in 1969, 1971, and 1972 (Richardson 1973, footnote 5, unpubl. data; Richardson and Pearcy 1977). The earliest that northern anchovy larvae were taken in those years was 19 June and the latest that small larvae (<10 mm) were collected was 10 August. Peak abundance, >100/10 m² or >1,000/1,000 m³ at a station, occurred only between 21 July and 6 August. The spawning season was estimated to last approximately from 15 June to 15 August, or 62 days.]
t_i = the time in days from spawning to hatching of the egg determined from the equation given by Zweifel and Lasker (1976) for incubation times for northern anchovy:

$$I_T = I_0 \exp\,[m(1 - \exp(-\beta T))] \qquad (6)$$

where $I_0 = 1861$
$m = -5.4572$
$\beta = 0.0626$
T = the mean temperature at 3 m depth at stations where northern anchovy eggs were taken, 15.18° C in 1975 and 16.09° C in 1976.

The Sette and Ahlstrom Egg Method assumes a constant egg production throughout the spawning season.

The Simpson Egg Method of estimating the number of eggs spawned in a season (E_s) was that given by Simpson (1959) as modified by Houde (1977). The cruise census estimate, C_k or C_{kr}, was used to determine the number of eggs produced per day during the spawning season

$$E_d = \frac{C_k}{t_i} \text{ or } \frac{C_{kr}}{t_i} \qquad (7)$$

where E_d = daily egg production
t_i is defined under Equation (5).

The seasonal estimate of egg production (E_s) was then determined by plotting the daily egg production against the middate of the cruise representative of the spawning season. The area under the resulting polygon (triangle in this case), determined by planimetry, was then equated with egg production for the entire spawning season. This method assumes a high egg production midseason tapering off to low production at the beginning and end of the spawning season. It approaches a normal distribution of egg production. For species with a short spawning season as in northern anchovy off Oregon and Washington, estimates obtained by this method are about one-half as large as those obtained by the Sette and Ahlstrom Egg Method.

The Saville Egg Method of estimating seasonal egg production (E_s) is based on Saville's (1956, 1964) approach. It assumes that egg production follows a normal distribution throughout the spawning season. A census estimate (C_k or C_{kr}) of eggs obtained from a cruise made during the spawning season represents a proportion of the area under a normal curve. If the duration and peak of the spawning season are known, seasonal egg production (E_s) can be estimated (Houde 1977) as:

$$E_s = \frac{C_k y_i}{x_i t_i} \text{ or } \frac{C_{kr} y_i}{x_i t_i} \qquad (8)$$

where y_i = the number of days in cruise i
x_i = the proportion of the area under the normal curve represented by cruise i
t_i is defined under Equation (5).

Duration of the spawning season is assumed to be 62 days, lasting from 15 June to 15 August (see D_i under Equation (5)). The spawning peak is assumed to be the middate, 15 July.

The Smith Larva Method of estimating spawning biomass (B) is modified from the method used

in the CalCOFI program (Smith 1972; Pacific Fishery Management Council footnote 2). It relates the census estimate (C_k or C_{kr}) of northern anchovy larvae to spawning biomass by means of a regression. Smith (1972) demonstrated that in the CalCOFI survey area the annual regional census estimate (sum of four quarterly estimates) of larvae is related to northern anchovy spawner biomass in the following way:

$$B_a = 0.098\, L_a \quad (9)$$

where B_a = anchovy spawner biomass in short tons

L_a = annual regional census estimate of larvae $\times 10^9$ which is the sum of the four quarterly census estimates.

This equation was based on yearly data from 1951 to 1966 and 1969, with the zero intercept forced, giving 18 data points. Data, upon which Smith's (1972) equation was based, can be used to obtain a modification of this relationship, applicable to this study, if certain assumptions are met, or can be accounted for: 1) the same relationship between census estimates of the number of northern anchovy larvae and northern anchovy spawning biomass exists in the northern subpopulation as in the central and southern subpopulations; 2) the larva census estimate obtained from one cruise at the time of peak spawning during the shortened spawning season in the northern subpopulation is equivalent to a quarterly census estimate made during the peak spawning period, i.e., winter or spring quarter (Ahlstrom 1967) in the central subpopulation; 3) conditions, primarily temperature, which influence development time and therefore length of planktonic life, are similar in the northern and central subpopulations for the time periods considered; 4) sampling in the two survey regions is similar; 5) spawning frequency during the time period considered, i.e., during one quarter in the central subpopulation and during the 2-mo spawning season in the northern subpopulation, is the same in both areas.

Data from the Pacific Fishery Management Council (footnote 2) on quarterly larva census estimates for the central subpopulation for winter and spring quarters (Table 1) were regressed on spawner biomass estimates for the years 1951 through 1966 and 1969, 1972, and 1975, with the zero intercept forced, giving 20 data points each.

$$\text{Winter quarter: } B_a = 614 + 0.152\, L_w \quad (10)$$
$$r^2 = 0.70$$

$$\text{Spring quarter: } B_a = 645 + 0.151\, L_s \quad (11)$$
$$r^2 = 0.72$$

where L_w = the winter quarterly regional census estimate of northern anchovy larvae

L_s = the spring quarterly regional census estimate of northern anchovy larvae.

Because Smith's (1972) equation yielded a spawning biomass estimate in short tons, the values obtained in Equations (10) and (11) are also in short tons and may be converted to metric tons (t) by multiplying by 0.9078. Larvae in my study were collected with a 0.333 mm mesh net instead of the 0.55 mm mesh silk net upon which CalCOFI larva census estimates are based (Lenarz 1972; Pacific Fishery Management Council footnote 2). To correct for the increased retention by the smaller mesh net, larva census estimates were divided by the factor given by Lenarz (1972):

$$C_k \text{ corrected} = \frac{C_k}{1.7} \text{ or } C_{kr} \text{ corrected} = \frac{C_{kr}}{1.7}. \quad (12)$$

Thus, in my study I assumed that

$$L_w = L_s = C_k \text{ (or } C_{kr}\text{) corrected.} \quad (13)$$

TABLE 1.—Census estimates (units $\times 10^9$) of *Engraulis mordax* larvae in the central stock for winter and spring quarters and spawner biomass estimates (in 10^3 short tons) of the central stock [from Pacific Fishery Management Council (text footnote 2) A.14 and A.15] from which Equations (10) and (11) were derived (see Methods section).

Year	Winter census	Spring census	Spawner biomass
1951	298	690	180
1952	407	457	156
1953	1,210	373	510
1954	4,469	988	768
1955	5,588	1,709	846
1956	1,911	1,206	485
1957	5,954	4,308	1,172
1958	8,114	5,236	1,479
1959	6,341	8,155	1,514
1960	7,552	7,547	1,540
1961	992	6,714	1,159
1962	4,814	23,567	2,986
1963	17,377	24,818	4,254
1964	8,941	14,383	2,901
1965	19,155	22,690	4,659
1966	15,103	15,865	3,572
1969	19,756	6,538	2,999
1972	8,213	14,335	2,784
1975	29,754	4,071	3,603

Yield Estimates

Because the northern anchovy stock under consideration is in a nearly virgin state, an estimate of potential yield can be obtained using Gulland's (1971) formula

$$Y_{pot} = XMB_0 \quad (14)$$

where Y_{pot} = maximum potential yield
X = a constant coefficient [0.6 for northern anchovy based on MacCall et al. (1976)]
M = instantaneous natural mortality rate [1.00-1.05 for northern anchovy based on MacCall et al. (1976) and Pacific Fishery Management Council (footnote 2)]
B_0 = mean virgin biomass, in this case spawning biomass.

SURVEY RESULTS

Hydrography and Plankton Volume

In all 3 yr, upwelling activity was observed along the coast, evidenced by the colder, <14° C water nearshore (Figures 3-5). This is a typical summer condition when winds blow mainly from the north, currents tend generally to the south, upwelling takes place in a narrow band along the coast with resultant offshore transport of surface waters (Wyatt et al. 1972; Smith 1974; Huyer et al. 1975; Ingraham and Hastings 1976; and others). Offshore, especially beyond the continental shelf, water temperatures were >14° C, well within the range for successful northern anchovy spawning and early development (Brewer 1976).

Salinity contours showed that all three surveys covered the inner bounds of the Columbia River plume, delineated by the 31‰ isohaline (Figures 3-5). The outer bounds of the plume, defined by the 32.5‰ isohaline (Barnes et al. 1972), were not encompassed. This plume is a persistent hydrographic feature off the Oregon coast in summer (Barnes et al. 1972). The Columbia River reaches maximum outflow in June and flows southerly, under the influence of prevailing winds and currents, as a plume of shallow (20-40 m deep), low salinity, warm water on top of the more saline and colder ocean water. It can extend as far as 800 km offshore and as far south as northern California. In 1976 the plume extended farther south and was closer to the coast than in 1975. In 1977 the central core of the plume was much reduced reflecting the extreme drought conditions of that year. High salinities, >33‰, along the coast were indicative of upwelling.

Chlorophyll concentrations at 3 m in 1975 and 1976 were greatest near the coast in regions of upwelling and generally decreased with distance from shore (Figures 3, 4). In 1975, relatively moderate concentrations extended beyond the continental shelf in the region of the lowest salinity plume water. This may be indicative of higher productivity associated with nutrient rich plume waters near the Columbia River mouth (Anderson 1972).

Of the 920 surface drifters released in July 1976, 24 or 2.6% were returned by 21 August 1976 (Figure 6). No additional returns were reported as of February 1977. All but seven of the returns were from the 2 km stations. All returns that had been released off Oregon indicated southward transport. Two returns from the 2 km station near the Columbia River indicated some transport into the river and one return showed northward movement. Three drifters released 46 km off Grays Harbor, Wash., were transported toward the coast while three drifters from the 2 and 9 km stations were transported moderate distances northward. The low number of returns (2.6%) probably reflects the offshore component of surface drift which is generally observed during the summer upwelling season (Wyatt et al. 1972; Huyer 1974).

Plankton volumes, which ranged from 30 to 4,726 ml/1,000 m³ in 1975 and 8 to 3,670 ml/1,000 m³ in 1976, were greatest on the continental shelf with the highest volumes (>2,000/1,000 m³) occurring at stations 2, 9, and 28 km from shore (Figures 3, 4). In these areas the plankton consisted largely of phytoplankton and ctenophores although at 9 and 28 km off Cape Perpetua, Oreg., in 1975 it consisted mainly of copepods and euphausiids. Nearshore low plankton volumes <100 ml/1,000 m³ were observed at the 2 km stations off Grays Harbor in both 1975 and 1976 and off the Columbia River in 1975. High plankton volumes appeared to be mainly associated with coastal upwelling with no obvious relationship to the Columbia River plume. However, plume waters are a near surface phenomenon while the plankton was sampled from 150 m to the surface possibly obscuring any relationship.

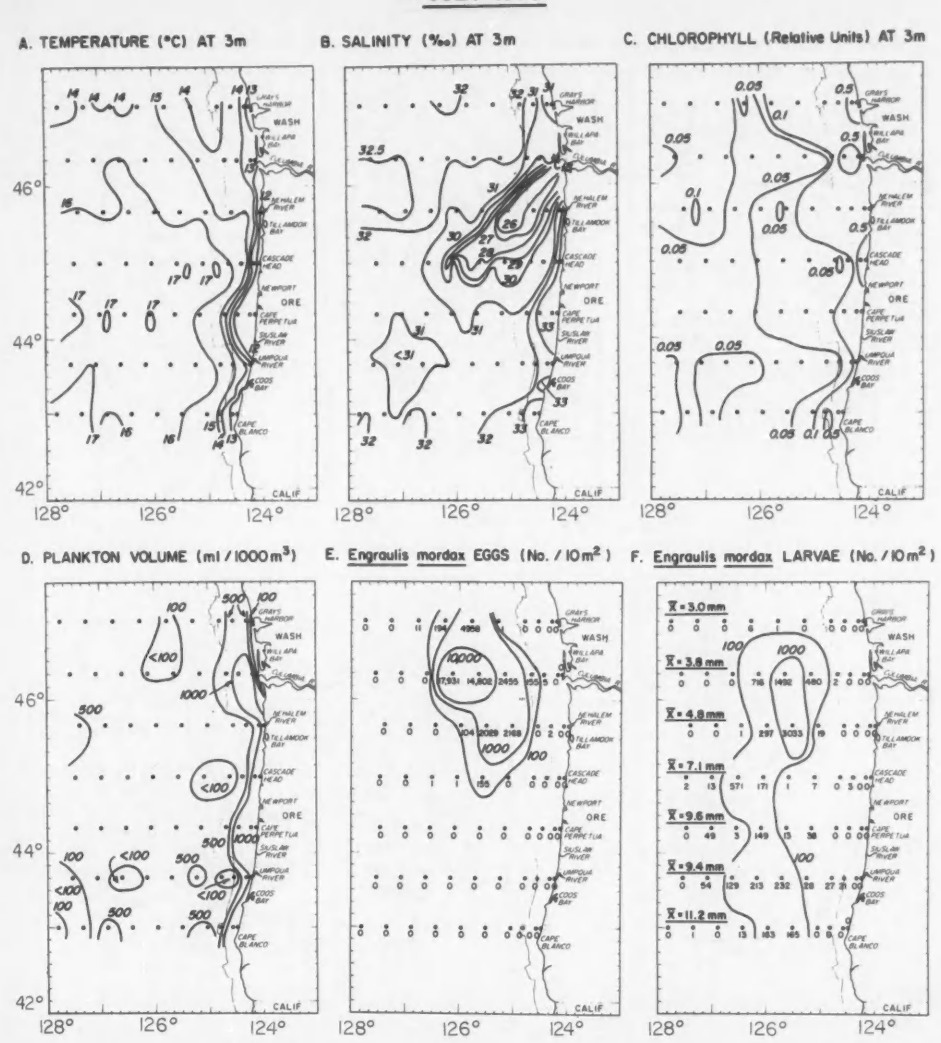

FIGURE 3.—Results from the July 1975 ichthyoplankton survey off Oregon and Washington: hydrography, plankton volume, *Engraulis mordax* eggs and larvae. One chlorophyll unit is equivalent to 46.3 μg coproporphyrin standard/l or 6.14 μg chlorophyll *a*/l. Mean standard length of northern anchovy larvae on each transect is listed along the left margin of F.

Eggs and Larvae

Northern anchovy eggs were taken at 17 and 23 of the 70 stations sampled in 1975 and 1976 (Figures 3, 4; Table 2). In 1975 the center of egg abundance was north of the Columbia River plume. Largest concentrations, up to 17,931 under 10 m² sea surface, occurred 120-157 km off the mouth of the Columbia River. In 1976, the center of abundance was located 83 km off the Oregon coast

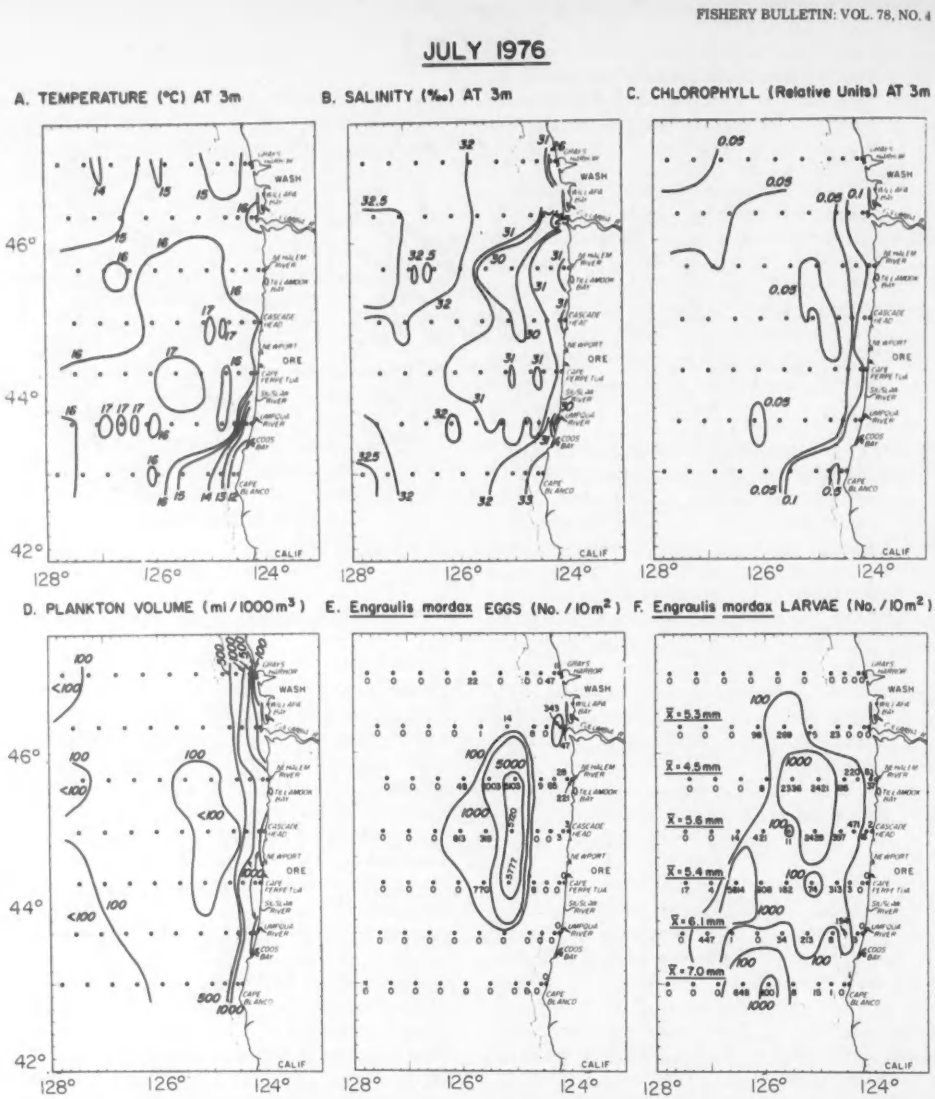

FIGURE 4.—Results from the July 1976 ichthyoplankton survey off Oregon and Washington: hydrography, plankton volume, *Engraulis mordax* eggs and larvae. One chlorophyll unit is equivalent to 46.3 μg coproporphyrin standard/l or 6.14 μg chlorophyll *a*/l. Mean standard length of northern anchovy larvae on each transect is listed along the left margin of F.

between the Nehalem River and Cape Perpetua within the Columbia River plume. The largest egg concentration, 5,777 under 10 m² sea surface, was one-third the highest concentration found in 1975. Overall mean egg abundance was 642 and 291 under 10 m² sea surface in 1975 and 1976, and at positive stations it was 2,645 and 886 under 10 m². In both years the egg distribution was bounded to the south and offshore but not to the north, although relatively few eggs were taken on the

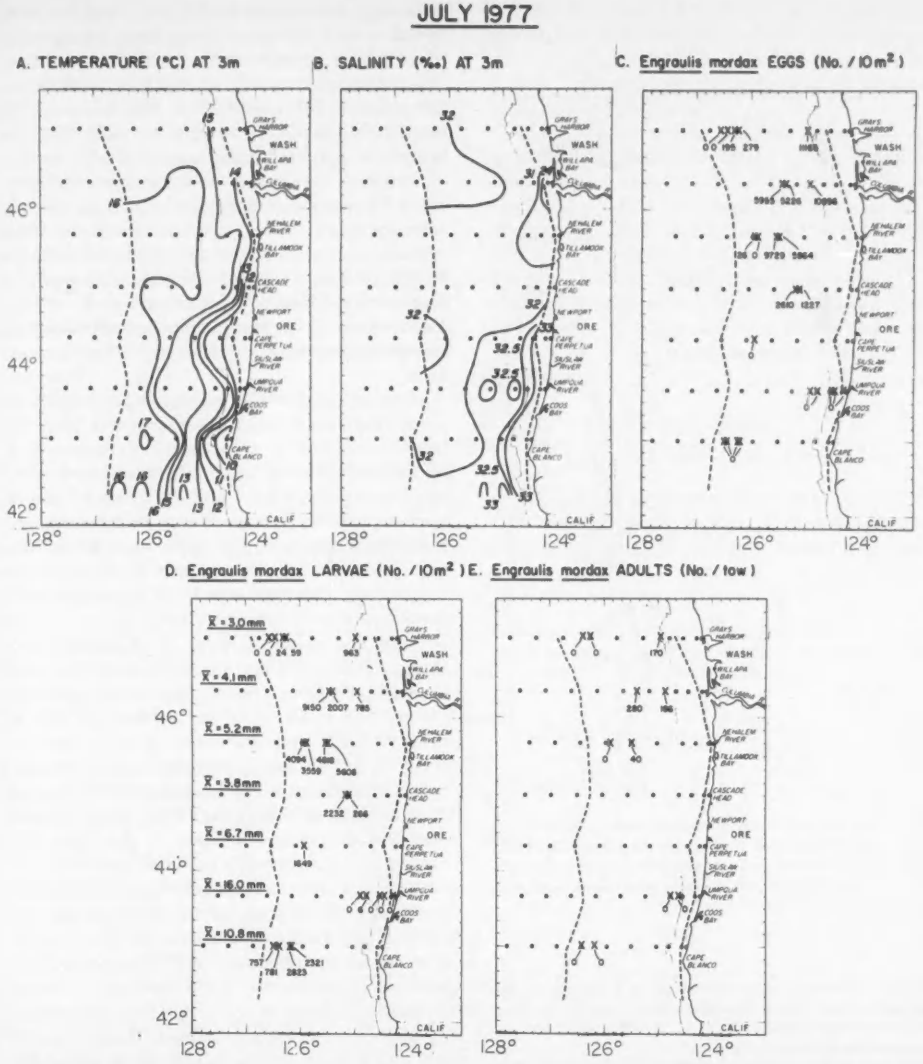

FIGURE 5.—Results from the July 1977 acoustic survey off Oregon and Washington: hydrography, *Engraulis mordax* eggs, larvae, adults. Values for adult catches are based on a 30 min surface tow of a pelagic trawl. Dotted lines delimit east and west cruise track boundary. On C and D, "X" indicates location of the only bongo samples taken during this cruise. On E, "X" indicates location of pelagic trawl stations. Mean standard length of anchovy larvae on each transect is listed along the left margin of D. Data in C and D courtesy of Methot (text footnote 11). Data in E from Smith (text footnote 10).

northernmost transect in 1976. No eggs were taken in regions of active upwelling and few were taken nearshore over the continental shelf except at the 9 km station just north of the Columbia River mouth in 1976 where a patch of warm, <16° C, surface water occurred. The farthest offshore

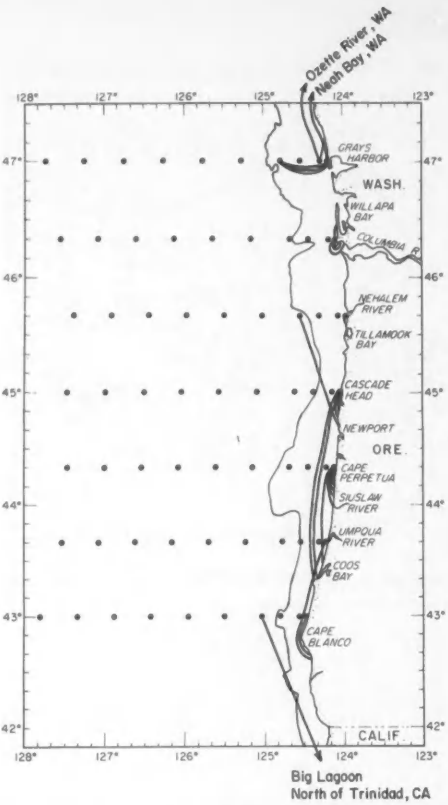

FIGURE 6.—Returns of surface drifters released at the sampling stations off Oregon and Washington during the July 1976 ichthyoplankton survey and returned by 21 August of that year. Lines represent drift paths from release point (sampling station) to return location. Depth contour is 183 m.

TABLE 2.—Summary of collection data on *Engraulis mordax* eggs and larvae off the Oregon-Washington coast from ichthyoplankton surveys conducted in 1975 and 1976. Seventy stations were occupied on each survey.

Item	10-18 July 1975	7-15 July 1976
No. positive stations		
Eggs	17	23
Larvae	33	40
Eggs or larvae	38	45
Eggs and larvae	12	18
Mean no. eggs/10 m²		
All stations	642.49	291.15
Positive stations	2,645.54	886.10
Mean no. larvae/10 m²		
All stations	115.89	278.73
Positive stations	245.82	487.78

that eggs were taken was 194 km and few were found beyond 157 km. All eggs were taken at stations where surface temperatures were >14° C. Mean temperature at 3 m depth at positive stations was 15.18° and 16.09° C and mean salinity was 30.69 and 30.07‰ in 1975 and 1976. Egg concentrations did not correlate with high surface chlorophyll levels and greatest concentrations were in regions of low plankton volumes. Although bongo samples were taken only at trawl stations during the acoustic survey in 1977 (Figure 5) catch trends of eggs were similar to the previous two surveys (Methot[12]). Northern anchovy eggs were taken only on the four northern transects in concentrations up to 11,165 under 10 m² sea surface.

Northern anchovy larvae were more widely dispersed than northern anchovy eggs with 33 and 40 positive stations in 1975 and 1976 (Figures 3, 4; Table 2). Thirty-eight and 45 stations had either eggs or larvae in 1975 and 1976 and 12 and 18 stations had both, respectively. In 1975, highest numbers of larvae, >1,000 under 10 m² sea surface, were found 120 km offshore, near and south of the highest egg concentrations. In 1976, greatest larva concentrations occurred 83 and 120 km offshore between the Nehalem River and Cascade Head, Oreg.; 194 km off Cape Perpetua; and 120 km off Cape Blanco, Oreg. Overall mean abundance was 115 and 278 under 10 m² sea surface in 1975 and 1976, and 487 and 245 under 10 m² at positive stations. In 1975 larvae occurred mainly in a corridor paralleling the coast beyond the continental shelf while in 1976 they were more widely distributed and also occurred closer to the coast. The sampling grid apparently bordered their center of abundance to the north and offshore but not to the south. As with the eggs, larvae were generally not found in regions of active upwelling. Mean length of larvae on each transect in 1975 increased progressively from 3.0 mm in the north to 11.2 mm in the south, evidence of drift south from the spawning center based on egg distributions and seasonal flow patterns. In 1976 mean length of larvae per transect increased from 4.5 mm off the Nehalem River to 7.0 mm off Cape Blanco but the trend was not as pronounced as in July 1975. This reduced trend may be partly a result of decreased northerly winds, evidenced by reduced upwelling, and reduced southward transport compared to 1975.

[12]R. D. Methot, Scripps Institution of Oceanography, Graduate Department, La Jolla, CA 92093, unpubl. data.

Also, based on egg distribution the spawning aggregation appeared more widely distributed in a north-south distance. Mean temperature and salinity at 3 m depth at positive stations in 1975 and 1976 were 15.66° and 15.96° C and 31.07 and 31.28‰, respectively. Distribution of larvae did not correlate with high surface chlorophyll levels and abundance was generally highest in regions of low plankton volume. During the acoustic survey in 1977, northern anchovy larvae were collected (Methot footnote 12) on each transect in concentrations up to 5,606 under 10 m² sea surface (Figure 5). No larvae were found in samples taken within 46 km of the coast. Mean length of larvae on each transect again showed an increasing trend toward the south.

Adults

During the acoustic survey in 1977, running ripe adult northern anchovy were collected on the three northern transects (lat. 47°02′ N, long. 124°56′ W; lat. 46°60′ N, long. 126°33′ W; lat. 46°19′ N, long. 124°54′ W; lat. 45°40′ N, long. 125°30′ W) between 56 and 130 km offshore (Figure 5). No adult northern anchovy were collected at trawl stations on the southern two transects. No trawls were made on the transects off Cascade Head or Cape Perpetua.

School concentrations, recorded by sonar, were presented by Smith (footnotes 10, 3). Based on sonar traces and results of the pelagic trawl catches, he concluded schools of spawning adult northern anchovy were centered 83 km offshore in the surveyed area and 37 km south of the Columbia River mouth with the inner edge about 37 km offshore and the western edge between 102 km and 130 km offshore. The northern edge was not defined above lat. 47° N and the southern edge was at lat. 44° N.

EGG AND LARVA CENSUS ESTIMATES

The total area represented by the survey in 1975 and 1976, was 148.81 × 10⁹ m². Census estimates of the total number of northern anchovy eggs and larvae in that area for each cruise are in Table 3.

TABLE 3.—Egg and larva census estimates (C_k and C_{kr}) and spawning biomass estimates (B) of *Engraulis mordax* in the survey area off Oregon and Washington in 1975 and 1976. Values of parameters used in the biomass estimating procedures are presented except those for K (proportion females) and F (mean fecundity) which are constants, 0.5 and 720. See Methods section for description of procedures and equations.

Spawning biomass estimating method	Year and season	Sette and Ahlstrom Census [1]C_k (units × 10^{11})	Sette and Ahlstrom Census corrected L_W or [2]L_S (units × 10^9)	Days represented by cruise D_i	Days included in cruise Y_i	Proportion of area under normal curve X_i	Time to hatch in days [3]t_i
Sette and Ahlstrom Egg Method	1975	121.98		62			2.73
[Equations (4) and (5)]	1976	54.89		62			2.43
Simpson Egg Method	1975	121.98					2.73
[Equations (4) and (7)]	1976	54.89					2.43
Saville Egg Method	1975	121.98			9	0.3335	2.73
[Equations (4) and (8)]	1976	54.89			9	0.3081	2.43
Smith Larva Method	1975 winter	22.22	1,307				
[Equations (10) and (11)]	1975 spring	22.22	1,307				
	1976 winter	52.06	3,062				
	1976 spring	52.06	3,062				

Spawning biomass estimating method	Year and season	Daily egg production [4]E_d (× 10^{11})	Seasonal egg production E_s (× 10^{11})	Spawning Biomass Estimate [5]B_a (tons)	Spawning Biomass Estimate [5]B (t)	Smith Census [6]C_{kr} (× 10^{11})	Spawning Biomass Estimate [7]B (t)
Sette and Ahlstrom Egg Method	1975		2,770.24		769,511	95.60	603,094
[Equations (4) and (5)]	1976		1,400.49		389,025	43.32	307,022
Simpson Egg Method	1975	44.68	1,316.27		365,631	95.60	294,933
[Equations (4) and (7)]	1976	22.59	708.87		196,909	43.32	170,694
Saville Egg Method	1975		1,205.82		334,951	95.60	262,506
[Equations (4) and (8)]	1976		659.84		183,289	43.32	144,654
Smith Larva Method	1975 winter			812,664	737,736	17.14	696,479
[Equations (10) and (11)]	1975 spring			842,357	764,692	17.14	723,705
	1976 winter			1,079,424	979,901	41.48	894,074
	1976 spring			1,107,362	1,005,263	41.48	920,001

[1]Equation (2).
[2]Equations (12), (13).
[3]Equation (6).
[4]Equation (7).
[5]Based on Sette and Ahlstrom Census.
[6]Equation (3).
[7]Based on Smith Census.

The Smith Census estimate was always lower than the Sette and Ahlstrom Census estimate. Both estimates were used to calculate spawning biomass of adults.

Larva abundance was not corrected for day-night catch differences. A correction factor could not be derived from the data. No consistent pattern of daytime avoidance was apparent based on cruise plots of night to day catch ratios for each millimeter length class as Houde (1977) demonstrated for clupeid larvae. If daytime avoidance did occur, larva census estimates would be low and in turn biomass estimates would be low. Net avoidance of larvae increases with age and since 94% of the larvae captured in 1975 and 98% in 1976 were ≤10 mm SL (standard length), errors due to avoidance should be small. Also, Smith (1972) made no day-night corrections for the CalCOFI program. Thus data from my study are comparable.

SPAWNING BIOMASS ESTIMATES

These biomass estimates apply only to that portion of the spawning population within the northern subpopulation off Oregon and Washington that was sampled in my survey area. In 1975, the egg concentration (Figure 3) was bounded inshore, offshore, and to the south, but the northern boundary was not encompassed. If major egg concentrations occurred north of the sampling area, the biomass estimates would be low. In 1976, essentially the entire egg concentration was bounded. In both 1975 and 1976, larva concentrations were bounded to the north and offshore, but not to the south. The estimates do not account for any additional spawning concentrations within the northern subpopulation should they exist.

The three methods of estimating spawning biomass based on egg abundance (Sette and Ahlstrom, Simpson, and Saville Egg Methods) include the assumption that northern anchovy spawn only one batch of eggs, those in the most advanced mode and upon which fecundity estimates are based, during the time sampled by the survey. This is particularly critical since the recent work by Hunter and Goldberg (1980) has indicated that a ripe adult northern anchovy can mature a batch of eggs and spawn once every 6 or 7 d in the central subpopulation. In this study the area in which northern anchovy eggs were collected was sampled in 5 d in 1975 and 6 d in 1976. It is assumed that the eggs collected represented no more than a single spawning, because batch 1 would hatch before batch 2 was spawned.

The three egg methods of estimating biomass do not take into account egg mortality. Rates of egg mortality in the ocean are unknown for northern anchovy and could not be determined in this study. Eggs could not be staged due to poor condition resulting from collection techniques. If mortality of spawned eggs were high and disintegration rapid (i.e., dead eggs not occurring in plankton samples), the estimates of total number of eggs spawned would be low and the resulting biomass estimates would also be low. However, Sette and Ahlstrom (1948) obtained similar biomass estimates for *Sardinops caerulea* using two techniques, one that involved aging of eggs and another, the Sette and Ahlstrom Egg Method used in my paper, that did not. Presumably egg mortality was not a major factor influencing their estimates. A similar situation may exist for northern anchovy which also has a relatively short-lived (2 or 3 d) egg stage.

Sette and Ahlstrom Egg Method

The egg census estimate (Table 3) for each cruise was divided by the duration of the egg stage, estimated to be 2.73 d in 1975 and 2.43 d in 1976, Equation (6), to obtain estimates of daily egg production. This value was then expanded to the number of days (62) represented by the cruise, Equation (5). Biomass estimates for each cruise were then obtained, Equation (4).

Estimated spawning biomass using the Sette and Ahlstrom Census was 769,511 t in 1975 and 389,025 t in 1976 (Table 3). Somewhat smaller values were obtained with the Smith Census 603,094 and 307,022 t. Since the method used to derive the Smith Census is merely a simplified version of the method used for the Sette and Ahlstrom Census, biomass estimates based on the latter may be better, at least for the egg data. Confidence limits (95%) based on variance estimates of egg abundance, using methods of Houde (1977), gave a range around the point biomass estimates of ±11-15% for all egg methods. However, the variance estimates were low and statistically not very precise because of the low number of data points and are thus not included here. The Sette and Ahlstrom Egg Method assumes a constant egg production throughout the 62-d spawning season. If egg production tapers off at the

beginning or end of the season, the biomass estimates would be high.

Differences in biomass estimates between the 2 yr based on eggs reflects the fact that more than twice as many eggs were collected in 1975 than in 1976. This could be the result of a decrease in spawning biomass between the years although small sample size is probably just as important. Biomass estimates based on eggs are likely to be more variable than those based on larvae. Northern anchovy is a schooling fish; therefore eggs released from spawning schools are clumped, resulting in a sample of high variance (Pacific Marine Fishery Management Council footnote 2).

Simpson Egg Method

Estimates of daily egg production, Equation (7), 44.68×10^{11} in 1975 and 22.59×10^{11} in 1976 using the Sette and Ahlstrom Census (Table 3) and 35.02×10^{11} and 17.83×10^{11} using the Smith Census, were plotted against the cruise middate. The area under the resulting triangle was then equated with egg production for the entire spawning season, $1{,}316.27 \times 10^{11}$ in 1975 and 708.87×10^{11} in 1976 with the Sette and Ahlstrom Census and $1{,}061.76 \times 10^{11}$ and 614.50×10^{11} with the Smith Census. Biomass estimates were then obtained with Equation (4).

Spawning biomass estimates were 365,631 t in 1975 and 196,909 t in 1976 using the Sette and Ahlstrom Census and slightly smaller with the Smith Census (Table 3). These biomass values are nearly one-half those obtained by the Sette and Ahlstrom Egg Method. This reflects the different assumption of this method regarding egg production where it is high in mid season and low at both ends.

Saville Egg Method

Egg production is assumed to follow a normal curve throughout the 62-d spawning season from 15 June to 15 August. Each cruise within that period represents a proportion of the area under that normal curve. In this study, each cruise was of 9 d duration and was made near the peak of the spawning period. In 1975 the cruise represented 33.35% of the curve and in 1976, 30.81%. Seasonal egg production was then estimated by Equation (8) and biomass by Equation (4).

Estimates of biomass using this method were smaller, 334,951 t in 1975 and 183,289 t in 1976 using the Sette and Ahlstrom Census, than in the two previous methods (Table 3). If egg production is skewed from a normal distribution, large errors could be introduced into the biomass estimate.

Smith Larva Method

This method of estimating spawning biomass assumes that a similar linear relationship exists between numbers of larvae and adult spawning biomass in both the central and northern subpopulations. Although this assumption seems reasonable, the recent fecundity estimate for northern anchovy off California, 340 eggs/g total female weight (Hunter and Goldberg 1980), is considerably less than the fecundity estimate obtained for northern anchovy off Oregon, 720 eggs/g total female weight (Laroche and Richardson 1981). These data indicate it would take more planktonic eggs to represent 1 g of fish in the northern than in the central subpopulation. It follows then that it would also take more pelagic larvae to represent 1 g of fish in the northern subpopulation given that spawning frequency and larval growth and mortality conditions are similar. Thus, biomass estimates obtained by this method may be too high.

Other assumptions of the method seem reasonable (see Methods section). The census estimate obtained from one cruise during the shortened spawning season in the north should be equivalent to a quarterly census estimate obtained during a peak spawning period in the south. Sometimes a quarterly estimate for CalCOFI is based on only one cruise, other times a mean of several cruises. However, my cruise dates were purposefully selected at the time of peak spawning. Sometimes CalCOFI quarterly cruises may be conducted near the beginning or end of a quarter and not necessarily at the peak of spawning. Thus larger numbers of smaller larvae may have been collected in our study, and the relationship between numbers of larvae and biomass may be biased to give a higher biomass estimate in the north.

In general, water temperatures at the time of peak spawning appear to be similar off Oregon and California (Ahlstrom 1959; Baxter 1967) so that growth rates and length of time in the water column are assumed to be similar. Methot (in press) demonstrated that growth rates of larvae in the two subpopulations are similar at similar temperatures.

Sampling techniques used in this study were

similar to those of the CalCOFI program (Kramer et al. 1972) except we used 0.333 mm mesh net on 70 cm bongos vs. 0.55 mm mesh on a CalCOFI net. The difference in mesh sizes can be corrected, Equation (12), but because of the reduced avoidance associated with bongo nets, larva catches may be relatively greater resulting in high census estimates and accordingly high biomass estimates.

Spawning frequency during the 2-mo spawning period in the northern subpopulation is unknown. Hunter and Goldberg (1980) indicated that northern anchovy in the central subpopulation may spawn a batch of eggs every 6 or 7 d during peak spawning. If northern anchovy off Oregon respond differently, additional error would be introduced into the biomass estimate. The higher fecundity of fish in the north may be balanced by less frequent spawning.

Spawning biomass estimates derived from the Smith Larva Method are based on larva abundance. Using the larva census estimates corrected for mesh size differences, Equation (12), biomass estimates were obtained by Equations (10) and (11). These estimates were 737,736 and 764,692 t in 1975 and 979,901 and 1,005,263 t in 1976 with the Sette and Ahlstrom Census and slightly less with the Smith Census, 696,479 and 723,705 in 1975 and 894,074 and 920,001 in 1976. In this case, since the Smith Census is based on procedures and data (Smith 1972) from which Equations (10) and (11) are derived, biomass estimates based upon it are probably better than those based on the Sette and Ahlstrom Census.

Because of diffusion and dispersion and length of the larval period (about 30 d compared with 2-4 d for eggs), larvae are more evenly distributed over a given geographic area than eggs and in turn yield a less variable biomass estimate than eggs (Pacific Fishery Management Council footnote 2). This may, in part, account for the smaller year to year difference in biomass estimates based on larvae compared with those based on eggs. Interestingly biomass estimates based on eggs decreased greatly from 1975 to 1976 while those based on larvae increased.

Most Probable Biomass

Spawning biomass estimates (Table 3) ranged from 262,506 to 769,511 t in 1975 and 144,654 to 1,005,263 t in 1976 (Table 3). The biomass estimate based on acoustic survey of adults in July 1977 was about 800,000 t (Smith footnote 3), using methods given by Smith (1970). A reasonable conclusion is that the actual spawning biomass of northern anchovy in the survey area laid or fluctuated between the extreme values in 1975 and 1976 (Houde 1977) and is probably <1 million t but >100,000 t. This line of reasoning is supported by the fact that the estimates from 1975 and 1976 (for a given method) are within twofold of each other and less than tenfold (for any method) from the acoustic survey.

These estimates only include mature spawning adult fish. Laroche and Richardson (1981) reported that northern anchovy in the northern subpopulation attain first sexual maturity at the end of the second year, i.e., in the third summer. Thus northern anchovy <2 yr old are not included in the estimates and may represent additional sizeable biomass. These immature fish are segregated geographically from spawning adults during the spawning season with the young fish occurring in nearshore coastal areas (Laroche and Richardson 1981).

Based on these estimates, spawning biomass of northern anchovy off the Oregon-Washington coast is less than that in the central subpopulation which had a mean estimate of around 3,631,200 t for 1965-72 (MacCall et al. 1976), although a recent population decline has been recorded in 1978 (1,183,771 t) and 1979 (1,564,139 t) (Stauffer 1980). My spawning biomass estimates are more comparable to that for the southern subpopulation of 544,680 t (mean for 1965-69) (MacCall et al. 1976).

YIELD ESTIMATES

Using Gulland's (1971) formula for potential yield to a fishery, Equation (14), with the range of instantaneous natural mortality rates of 1.0-1.05, estimates for a biomass of 144,654 t are 86,792-91,132 t. For a biomass of 1,005,263 t they are 603,158-633,316 t. These potential yield estimates are about 60% of the spawning biomass, which may be dangerously high values for a species known to undergo large year-to-year fluctuations in abundance.

Recommendations for harvest quotas by the northern anchovy management plan for the central subpopulation called for a more conservative yield estimate of 70% of one-third, or about 23%, of the spawning biomass in excess of 907,800 t (Pacific Fishery Management Council footnote 2).

At an estimated spawning biomass of 3,631,200 t (MacCall et al. 1976) the harvest quota would be 635,400 t or approximately 17% of the total spawning biomass. At the recent reduced biomass level of 1,564,100 in 1979, the optimum yield established for the 1979-80 season in the U.S. Fishery Conservation Zone was 153,100 t (Stauffer 1980), equivalent to only 10% of the total spawning biomass.

Thus the actual realizable yield and in turn the feasibility of establishing a fishery on this northern stock of northern anchovy is difficult to assess. Northern anchovy are considered to be important forage items for fishes such as salmon and albacore off Oregon and Washington but northern anchovy biomass actually consumed by these species has not been adequately estimated. Northern anchovy are also important items in the diet of marine birds. Weins and Scott (1975) estimated that four species of marine birds consume 28,000 t of northern anchovy annually off Oregon.

If the northern anchovy stock off Oregon and Washington could support a harvest of 10% of the total biomass, as in the recent quotas on the reduced biomass for the central subpopulation, a yield of about 14,465-100,526 t might result. If this is reasonable, the feasibility of establishing such a fishery still remains to be determined. Feasibility partly depends on distribution patterns and habits of the stock and on economic considerations, the latter of which is beyond the scope of this paper. Seasonal patterns of distribution were discussed by Laroche and Richardson (1981). The most compact aggregations appear to occur during the spawning season in the offshore spawning center. However, school sizes appear to be small. Smith (footnote 3) estimated that half of the northern anchovy schools counted during the acoustic survey in July 1977 were <4 t and only 1.1% were over 64 t. Small school size could be a deterrent to fishery development.

COMPARISON OF NORTHERN AND CENTRAL SUBPOPULATIONS

Important ecological differences exist between the northern and central subpopulations of *E. mordax* with respect to spawning times and locations and associated environmental parameters. Off California, spawning takes place throughout the year (Figure 7) with a peak occurring between January and April (Smith and Richardson 1977). Off Oregon, spawning takes place over a 2-mo period (Figure 7) with a peak in July, based on the collection of small larvae (Richardson 1973, footnote 5). These differences in peak spawning times certainly contribute to reproductive isolation.

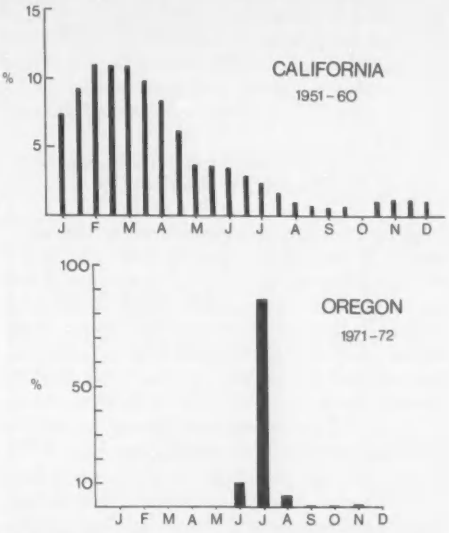

FIGURE 7.—Spawning cycle of *Engraulis mordax* off California and Oregon. Upper graph is after Smith and Richardson (1977). Lower graph is based on catches of northern anchovy larvae given by Richardson (text footnote 5).

Off California (Figure 8), at the initiation of peak spawning southward flow of the California Current is minimal (Saur 1972) with resulting minimal larval transport south away from the spawning area; temperature at 10 m depth (Lasker and Smith 1977) is reaching minimum values in the annual cycle; upwelling is minimal but increasing (Bakun 1973); day length is beginning to increase after the shortest day in December. In contrast, off Oregon (Figure 9), at the time of peak spawning, current flow to the south is at a maximum (Huyer 1977); surface temperatures (Johnson 1961) are reaching maximum values in the yearly cycle (excluding the colder waters of the nearshore upwelling zone); upwelling activity is at a maximum (Bakun 1973); day length is beginning to decrease after the longest day in June.

Off California (Figure 10), spawning takes place closer to the coast (Smith and Duke[13]) than off

[13]Smith, P. E., and S. Duke. 1975. Nearshore distribution of northern anchovy eggs and larvae (*Engraulis mordax*). NOAA NMFS, Southwest Fish. Cent., Admin. Rep. No. LJ-75-58, 15 p.

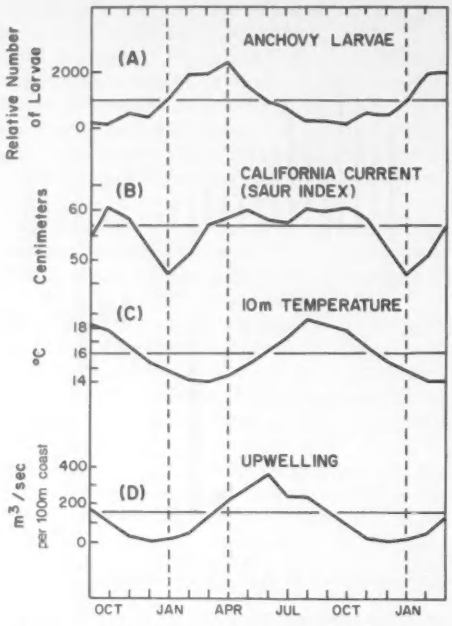

FIGURE 8.—Yearly cycle of *Engraulis mordax* larva abundance and selected environmental parameters [mean annual cycles (1953-60)] off California (reproduced from Lasker and Smith 1976). A) Larva abundance. B) California Current strength indicated by sea level difference approximations (Saur 1972). C) Temperature at 10 m depth. D) Upwelling (Bakun 1973). Dashed lines indicate period of peak spawning between January and April. Horizontal lines are for reference only.

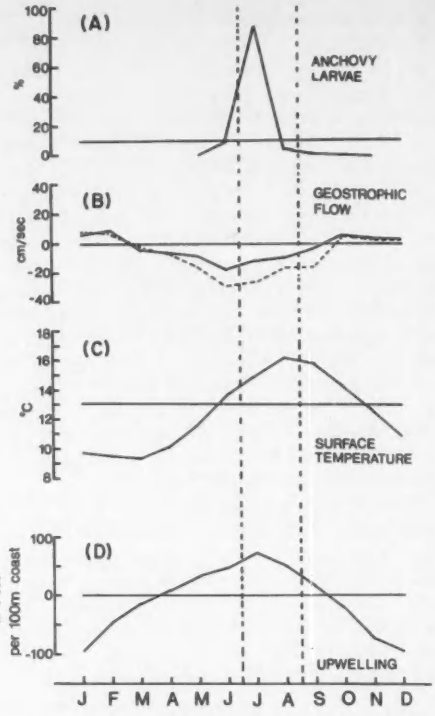

FIGURE 9.—Yearly cycle of *Engraulis mordax* abundance and selected environmental parameters off Oregon. A) Larva abundance in 1971-72 off Newport, Oreg. (Richardson text footnote 5). B) Estimates of alongshore geostrophic flow between 28 and 46 km off Newport at the surface (solid line) and 50 m (dotted line) after Huyer (1977). C) Monthly mean of surface temperatures recorded in six 2° squares off Oregon and Washington (lat. 42°-48° N; long. 124°-128° W) from 1947 to 1958 from Johnson (1961). D) Mean monthly values of upwelling indices for the 20 yr period 1948-67 at lat. 45° N, long. 125° W from Bakun (1973). Dashed lines indicate period of peak spawning. Horizontal lines are for reference only.

Oregon. Relatively little nearshore spawning takes place in the coastal upwelling zone off Oregon which is probably related to the low water temperatures there during the spawning season. Lasker (in press) demonstrated that upwelling may disperse proper-sized food particles, mostly dinoflagellates, and thereby reduce survival of first feeding northern anchovy larvae. These dinoflagellates are replaced by smaller diatoms which are nutritionally inadequate for survival of northern anchovy larvae.

RELATIONSHIP WITH COLUMBIA RIVER PLUME

Data from this study and that by Richardson (1973) provide evidence that a northern anchovy spawning center within the northern subpopulation is closely associated with the Columbia River plume. Reasons for such an association may be related to conditions necessary to induce or trigger spawning in adults or conditions necessary for the survival of the eggs and larvae. Increased river flow and plume size, associated with snow melt and day length, may provide a cue for the offshore spawning migration of adults. Temperature may not be a major factor in the association as both oceanic and plume waters warm to temperatures >13° C (Johnson 1961) needed for spawning, although plume waters warm earlier (Owen 1968).

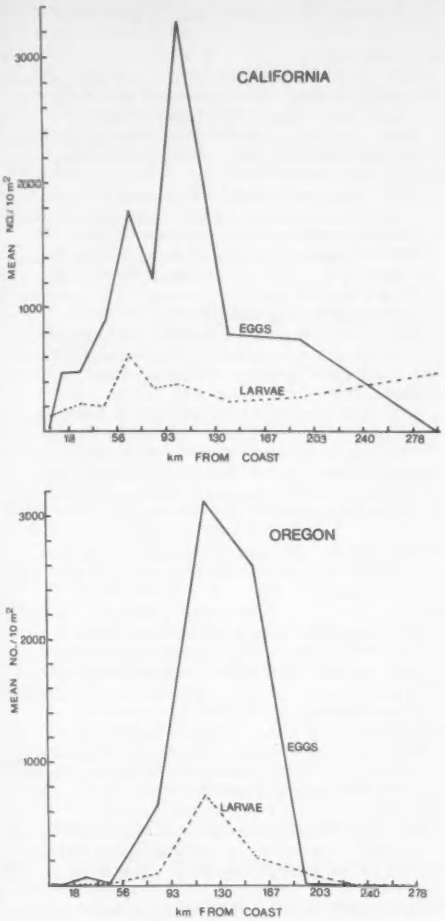

FIGURE 10.—Abundance of *Engraulis mordax* eggs and larvae with distance from the coast off California and Oregon. Upper panel based on data collected off Point Arguello, Calif., in January, April, and July 1964 (Smith and Duke text footnote 13). Lower panel data collected off Oregon and Washington in July 1975.

The plume may provide an optimal environment, in terms of stability and productivity particularly within 100 km or so from the river mouth (Anderson 1972; Barnes et al. 1972), to insure good feeding conditions and enhance survival of first feeding larvae. Such an environment may not exist in the less productive ambient oceanic water or the highly productive but too cold and dynamic coastal upwelling zone. Unfortunately data on type and availability of potential food items in the plume, which would help validate or refute this hypothesis, are not available.

LARVAL TRANSPORT AND JUVENILE NURSERIES

Because of the obvious southward transport of larvae away from the spawning center off Oregon and Washington and the later occurrence of juveniles in Oregon bays and rivers where spawning is apparently rare or unsuccessful, questions arise about return mechanisms. The deep (bottom third of water column) northward flowing countercurrent that develops in late summer beneath southward flowing surface waters (Huyer et al. 1975) could provide a mechanism for reduction of southward transport if larvae utilize it by migrating vertically. Unfortunately we have no depth distribution data on the larvae related to the depth of the shear layer between currents off Oregon to demonstrate this. However, if northern anchovy larvae come to the surface at night to gulp air and conserve energy, as off California (Hunter and Sanchez 1977), then southward and offshore transport would be enhanced, at least at night. Changing wind patterns in the fall from northerly to southwesterly (Wyatt et al. 1972) result in a shift in surface currents from southward to northward, cessation of upwelling, and an onshore drift of surface waters which may contribute to a northerly onshore movement of juveniles. Also, northern anchovy spawned later in the season may not be transported as far south as those spawned earlier and thus would not have to travel as far to return to northern bays and rivers.

An additional offshore spawning center to the north would help explain recruitment of juveniles to the Oregon rivers but there is no evidence for the existence of one, as discussed earlier.

The southward transport of larvae may provide an avenue of gene flow from the northern to central subpopulation.

OTHER SPAWNING CENTERS

Whether the area off the Columbia River is the primary or only spawning center for northern anchovy in the northern subpopulation is unknown. No evidence of spawning to the north exists at least in offshore waters. Also, no evidence is avail-

able for a major spawning center to the south off northern California although that area has not been sampled intensively. It is not known where ripening northern anchovy go after they leave Humboldt Bay in June (Waldvogel 1977), i.e., whether they go north to spawn near the Columbia River plume or whether they spawn off northern California.

Some evidence indicates that another spawning center may occur in the Strait of Georgia. Ripening adults (Pike 1951) and larvae as small as 11 mm (Robinson footnote 6) have been collected there. The environment created by the Fraser River may share similarities with that of the Columbia River plume in terms of stability and productivity (Waldichuk 1957). Thus the region may provide another suitable spawning environment. Additional sampling would be needed for adequate documentation. If a second major spawning center were defined in this region, it would be interesting to investigate the degree of mixing between Columbia River-spawned and Fraser River-spawned northern anchovy.

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VOLUNTARY SWIMMING SPEEDS AND RESPIRATION RATES OF A FILTER-FEEDING PLANKTIVORE, THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE)

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ABSTRACT

Voluntary swimming speeds and respiration rates of a group of adult Atlantic menhaden (mean wet weight = 302 g) were measured before, during, and after a 7-hour feeding period, during which the diatom *Ditylum brightwelli* was made available at a constant rate. Total ration for the 12 fish ranged between 9.60 and 94.79 g dry weight. Temperature was 20°±1° C. In the absence of food, the routine swimming speeds and respiration rates of the menhaden were: mean ± 95% confidence limits = 12.2±1.6 cm per second (0.47±0.06 body lengths per second), and 0.10±0.009 mg O_2 per gram per hour. During feeding the fish increased their voluntary swimming speed 2.4- to 3.5-fold, and their respiration rates 2.2- to 5.4-fold above the routine rates, depending on the concentration of plankton in the water. There was a linear relationship between $\log_{10}$ respiration rate and mean swimming speed during the feeding and the postfeeding periods. During feeding, the metabolic cost per increment in swimming speed was about 2.5 times higher than the cost of swimming in other species; this is believed to reflect a high energetic cost of filter feeding. There was an approximately hyperbolic relationship between the voluntary swimming speed of the Atlantic menhaden, and the phytoplankton chlorophyll *a* concentration in the water. The swimming speed and respiration rate of the fish remained constant as long as the input of phytoplankton into the tank continued at a constant rate. After feeding, the activity levels and respiration rates of the menhaden quickly returned to prefeeding routine rates.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling, filter-feeding planktivore (Peck 1894; Durbin and Durbin 1975) which supports a major commercial fishery along the Atlantic coast of the United States.

The present study investigates voluntary swimming speeds and oxygen consumption rates of Atlantic menhaden before, during, and after a 7-h period during which the fish were fed a ration of the diatom *Ditylum brightwelli*. During this period the plankton was made available at a constant rate, so that feeding was continuous and the ingestion rate was constant. The prolonged feeding was designed to reproduce, as much as possible, natural feeding conditions for menhaden. During these experiments ammonia and dissolved organic nitrogen excretion rates, feces production rates, and assimilation efficiencies were also measured and will be reported in a second paper. These studies are part of a larger effort to determine the energy budget of Atlantic menhaden in Narragansett Bay, R.I.

METHODS

Adult Atlantic menhaden were dipnetted from a commercial purse seine, 2-3 min after it had been set around a school. These fish were transferred to a round, 1.2 m diameter tank and brought in good condition to the laboratory. There the fish were maintained outdoors, in a circular fiber glass tank 1.85 m in diameter and 0.76 m deep, supplied with flowing unfiltered seawater. The tank was protected by a large fiber glass canopy.

Five days after capture, the number of fish in the tank was reduced to 25. Once a day the fish were fed a ration of Rangen's[3] salmon feed, size 00 powder, equivalent to 3% of their dry body weight per day. Within 3 wk all fish fed readily in the tank. The fish were held for 6 wk before use in experiments. During this period, the tank was cleaned every day, and preliminary trials were carried out. This enabled the fish to become accustomed to routine sampling procedures, to the presence of observers near the tank, and also to the presence of a clear Plexiglas cover, which was lowered onto the surface of the tank water during respiration mea-

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surements. The experiments were conducted in the same tank in which the fish were maintained. This removed two potential problems: first, the possibility of injury to the fish as a result of frequent handling; and second, the possibility of stress resulting from recent handling and transfer of the fish to an unfamiliar tank. Stress has been shown to affect the respiration rate and swimming performance of schooling fishes (i.e., Skazhina 1975; Hartwell and Otto 1978).

One week before the experiments were begun, one-half of the fish were removed for length and weight determination, leaving 12 Atlantic menhaden in the tank. We have found that 12-15 adult fish is an optimum number for a tank of this size; fewer fish begin to show signs of stress, whereas more fish begin to interfere with each other during feeding. Experiments were carried out between 26 July and 9 September 1977. At the end of this period the fish were sacrificed for length and weight determination. All fish appeared to be in excellent condition thoughout the experimental period, and showed no evidence of injury or disease.

Experimental Procedure

The experiments were carried out at 20°±1.0° C and a salinity of 31‰. Prior to each experiment, the bottom and walls of the tank were thoroughly cleaned with a wire brush. The fish were fed their normal ration, and then deprived of food for 36 h until the beginning of the experiment to permit evacuation of the intestine and to avoid any effect of the previous meal on the metabolism of the fish. During this 36-h period, the seawater inflow was filtered through a GAF polypropylene bag filter of 5 μm nominal pore size. Feces from the last meal were periodically siphoned from the tank. On the evening before the experiment, the tank walls were again scrubbed and the tank rapidly flushed several times with filtered seawater.

Each experiment was begun at approximately 0630 h, with an initial baseline measurement of respiration rate and voluntary swimming speed of the unfed fish. Plankton was then added to the tank at a constant rate during a 7-h period from approximately 0800 to 1500 h. During each experiment, respiration rates and voluntary swimming speeds were measured on 10 occasions, termed "measurements," which lasted for about 1 h when the fish were feeding, and 1½-2 h when they were not. These measurements correspond to the following periods: no. 1, initial (unfed for 36 h); no. 2-4, feeding during the 7-h period of food input; no. 5, the transition from feeding to postfeeding; no. 6-8, during the first 10 h following feeding; and no. 9 and 10, the next morning, 15-20 h after feeding.

To prevent an excessive accumulation of ammonia in the tank when the fish were fed the larger rations, the tank was flushed briefly with filtered water at the conclusion of feeding.

Food

The solitary diatom *Ditylum brightwelli* was used as food in the experiments. These large cells (~80 μm long) are readily eaten by menhaden. Phytoplankton was raised in outdoor batch cultures. Narragansett Bay water was filtered into 400 l fiber glass tanks, using a series of four cartridge filters culminating in a Gelman 0.45 μm membrane filter, and then enriched to the level of Guillard's F/2 (Guillard and Ryther 1962).

Large volumes (up to 2,500 l) of culture were raised for each experiment, and it was necessary to concentrate the cells before feeding them to the fish. Since the duration of the feeding period was 7 h, the culture was divided into seven batches of equal volume. Each batch was concentrated by gentle back filtration into a volume of 18 l, which was then subsampled by filtering onto a precombusted glass fiber filter for determination of the C and N concentration (Hewlett Packard Model 185B CHN Analyzer). On several occasions additional subsamples were centrifuged to form a pellet, from which the water was aspirated off, and the C, N, ash (combustion at 475° C for 4 h), caloric (Parr adiabatic bomb calorimeter), and Si (Durbin 1977) contents were determined. Each 18 l batch of food was slowly siphoned into the tank over a 1-h period, to provide an approximately constant rate of input of food. By changing the concentration of plankton in these batches, different concentrations of food in the tank and different ration sizes could be obtained. The volume of water added with the food was balanced by the volume removed during sampling, and thus the volume in the tank (1,400 l) remained approximately constant. The chlorophyll *a* concentration in the tank was also periodically determined by fluorometry (Yentsch and Menzel 1963; Lorenzen 1966).

Turbulence produced by the fish stirred the tank and kept the plankton in suspension. The Atlantic menhaden were estimated to filter 13-20% of the tank volume per minute, removing the *D.*

brightwelli with an efficiency of about 25% (Durbin and Durbin 1975).

Respiration Rate

Oxygen consumption by the fish was determined by closed system respirometry. The water in the tank was sealed from contact with the atmosphere by means of a circular cover made of clear 1.2 cm Plexiglas, suspended on pulleys over the tank, which could be gently lowered onto the water surface. Replicate water samples for oxygen determinations (Strickland and Parsons 1972) were siphoned from the tank through a sampling port every 12 min during feeding measurements, and every 20 min during nonfeeding measurements. The precision of the method was ±0.019 mg O_2/l. Measurements of oxygen from different locations in the tank demonstrated that the movement of the fish kept it well mixed at all times. Control measurements on the tank, filtered seawater, and tank water after the addition of phytoplankton demonstrated that these did not contribute significantly to the change in oxygen content of the water during respiration measurements. The oxygen level in the tank was not allowed to drop by more than 2 mg/l during any measurement; between measurements, the lid was raised off the surface of the water, and air was bubbled through the airstones along the tank walls. The decline of oxygen in the tank with time was linear, with a correlation coefficient of 0.98 or better in all cases; the mean respiration rate of the fish was calculated from the slope of this regression. Ninety-five percent confidence limits (CL) were computed for the slope and used to calculate the 95% CL for the respiraton rate in each measurement. Respiration rates are reported as milligrams oxygen consumption per gram wet weight of fish per hour (mg O_2/g per h).

Swimming Speed

During the respiration measurements the swimming behavior of the fish was recorded with a Sankyo ES-44XL 8 mm movie camera, equipped with a wide angle lens and a remote control and mounted above the tank. The fish were photographed with Kodak Ektachrome 160 film, exposed at 9 frames/s. Paired 10 s shots, 1 min apart, were taken every 6-10 min while the fish were feeding, and every 15-20 min when they were not feeding. Films were later analyzed using a Kodak Model MPG-TH microfilm reader at a magnification of 34×. A sheet of clear acetate was placed over the viewing screen, and the location of each fish was plotted at every fifth frame (the corresponding time interval at 9 frames/s = 5/9 s) when the fish were feeding and swimming rapidly, and every 10th frame (or, every 10/9 s) when the fish were not feeding and swimming slowly. These measurements were then converted to swimming speed in centimeters per second and body lengths (BL) per second. Vertical travel by the fish, which was not corrected for in this method, was negligible since the fish tended to maintain themselves at middepth in the water column.

During each measurement of oxygen consumption, an average of 680 observations of swimming speed were obtained. The average swimming speed during each measurement was determined from the mean of all observations ±95% CL. The distribution of swimming speeds within each measurement was compared with a normal curve. Measurements were compared by first testing for homogeneity of variance, and when appropriate the significance of the difference between means was tested using analysis of variance. When variances were nonhomogeneous, differences between means were tested according to a nonparametric test.

The mean values of each measurement were used to determine the relationship between swimming speed and respiration rate. Measurements were grouped into three categories: initial and final (unfed), feeding, and postfeeding. In the latter two categories there was a linear relationship between swimming speed and log oxygen consumption. Predictive regressions of Y on X are presented to permit the comparison of present results with those in earlier studies. However, we also present the functional regressions (GM) (Ricker 1973), which represent the geometric mean of the regression of Y on X and the reciprocal of the regression of X on Y. Although there has been some controversy on the subject (Jolicoeur 1975; Ricker 1975) the functional regression nevertheless appears to be the preferable method of describing the data. Differences in the slopes and elevations of the regressions were tested for significance by covariance analysis.

RESULTS

The menhaden were 3 yr old, with a mean fork length of 25.8 cm (range 23.0-27.9 cm), a mean wet

TABLE 1.—Basic data on feeding experiments with a school of 12 Atlantic menhaden, total wet weight = 3,624 g. Oxycalorific coefficient used was 4.7 cal/ml of oxygen consumed (Kleiber 1961). Column numbers, in brackets, are for text reference.

Experiment no. (1)	Total ration		Total respiration in excess of routine during the 7-h feeding period			Total respiration in excess of routine during the postfeeding period		
	G dry wt (2)	Kcal (3)	MgO_2 (4)	Kcal (5)	% of ration kcal (6)	MgO_2 (7)	Kcal (8)	% of ration kcal (9)
6	94.79	177.4	10,220	33.62	19.0	1,812	5.96	3.36
4	86.93	162.7	10,075	33.15	20.4	2,040	6.71	4.13
5	67.46	126.3	9,640	31.72	25.1	1,634	5.38	4.26
9	27.64	51.7	5,871	19.32	37.4	286	0.94	1.82
7	20.76	38.9	4,711	15.50	39.8	315	1.04	2.66
8	15.43	28.9	3,914	12.88	44.6	496	1.63	5.65
10	9.60	18.0	2,979	9.80	54.4	573	1.89	10.47

weight of 302 g (range 248-346 g), and a mean dry weight of 104 g.

The food rations ranged from 0.79 to 7.8% of the dry weight of the fish, and thus during the 7-h feeding period the fish fed at rates equivalent to 0.11-1.11% of their dry weight per hour (Table 1).

In a filter feeder such as the Atlantic menhaden, the food ration obtained depends on the volume of water filtered, corrected for the filtration efficiency of the gill rakers. The volume filtered is essentially cylindrical, with cross-sectional area equal to the area of the fish's open mouth, and length equal to the distance swum by the fish in a unit of time. It is shown below that the fish swam at about the same average speed during feeding, and since all fish were of similar size, each fish filtered an approximately equal volume of water during the 7-h feeding period. Thus we assume that each fish obtained the same proportion (1/12) of the plankton added to the tank.

The behavior of the fish followed the same general pattern in all experiments (Figures 1, 2). The voluntary swimming speeds and respiration rates of the fish were low during the initial measurement and then abruptly increased several fold over the initial rates during feeding. When the input of food was stopped, the fish rapidly filtered the remaining plankton from the water, decreasing their swimming speed and respiration rate as the plankton levels dropped. During the postfeeding period there was a gradual return to prefeeding activity levels and respiration rates, a transition which was completed before the final two measurements on the following morning.

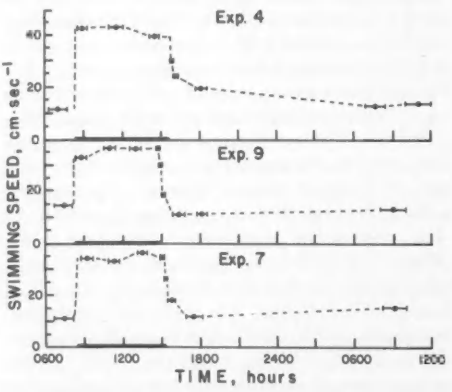

FIGURE 1.—Mean voluntary swimming speed of a school of 12 Atlantic menhaden before, during, and after a 7-h period (indicated by the heavy line on the *x*-axis) during which they were fed, at a constant rate, a ration of the diatom *Ditylum brightwelli*. Three representative experiments are shown, in which total rations were: no. 4, 162.7 kcal; no. 9, 51.7 kcal; no. 7, 38.9 kcal. The 95% confidence limits were enclosed by the symbols; horizontal bars indicate the duration of each experiment.

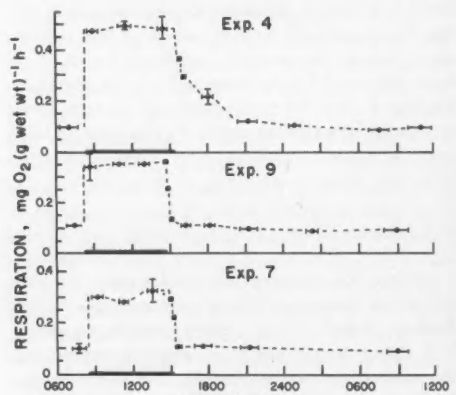

FIGURE 2.—Mean respiration rate for Atlantic menhaden in the measurements presented in Figure 1. The 95% confidence limits are shown by vertical bars when they exceed the size of the symbol.

In most measurements the distribution of swimming speed observations showed small but statistically significant ($\chi^2 < 0.01$) departures from normality. These usually took the form of a slight positive skewness, and leptokurtosis (data values concentrated in the region of the mean).

The variance of the swimming speed, which included the variability shown by each individual fish, as well as differences among fish, was positively correlated with the mean. However, the coefficient of variation revealed that the fish were relatively more variable in their swimming behavior when they were not feeding (Figure 3). These results confirmed qualitative observations during the experiments that the fish were least excitable, and most consistent in their swimming behavior, when they were engaged in feeding.

With the exception of measurement no. 5, which bracketed the transition from feeding to postfeeding, the fish were very consistent in their swimming behavior and respiration rate during individual measurements. Thus the 95% CL about the estimates of mean respiration rate and swimming speed during each of the measurements were small, averaging ±8.9% of the mean respiration rate and ±2.3% of the mean swimming speed.

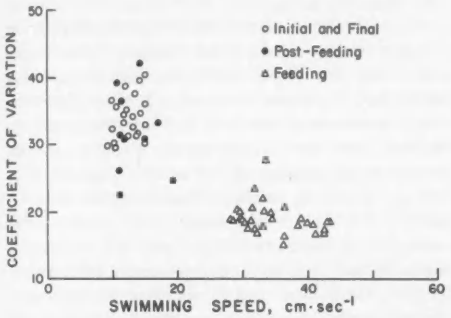

FIGURE 3.—Relationship between mean and coefficient of variation ($\sigma/\bar{x}$ [100%]) in the swimming speeds of a school of 12 Atlantic menhaden during the initial and final, feeding, and postfeeding measurements.

Initial and Final Measurements (No. 1, 9, 10)

These may be termed "routine" (Fry 1957) since the fish were unfed and spontaneously active. During these measurements the fish swam slowly about the tank without showing any strong schooling patterns. The mean swimming speeds and respiration rates were very similar during the initial and final measurements (Table 2). The range among the mean voluntary swimming speeds of the measurements was also fairly small, 10.5-15.2 cm/s (0.41-0.59 BL/s) (Figure 4). The range among

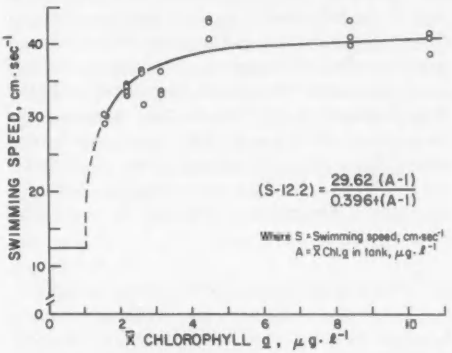

FIGURE 4.—Hyperbolic relationship between voluntary swimming speed (S) of a school of 12 Atlantic menhaden feeding on *Ditylum brightwelli*, and chlorophyll *a* concentration in the water (A). The three measurements of mean swimming speed obtained during the 7-h feeding period of each experiment are plotted as a function of the mean chlorophyll *a* concentration during each experimental feeding period.

TABLE 2.—Swimming speeds (S) and respiration rates (R) of Atlantic menhaden in the feeding experiments and their regression equations.

Measurements (periods)	Mean ± 95% confidence limits: Swimming speed cm/s	Respiration rate mg O_2/g per h
Initial (no. 1)	12.2±1.6	0.10 ±0.009
Final (no. 9, 10)	13.4±1.2	0.093±0.007

	Derived regressions: Predictive		Functional (GM)	
Feeding (no. 2, 3, 4)	$\log_{10}R = 0.0271\ (S) - 1.446$ ($r = 0.918$, SE slope = 0.0026)	Equation (2)	$\log_{10}R = 0.0295\ (S) - 1.534$	Equation (3)
Postfeeding (no. 6, 7)	$\log_{10}R = 0.0293\ (S) - 1.276$ ($r = 0.856$, SE slope = 0.0062)	Equation (4)	$\log_{10}R = 0.0342\ (S) - 1.342$	Equation (5)

the respiration rates was similarly narrow and did not show any clear relationship with swimming speed (Figure 4).

Feeding Measurements (No. 2, 3, 4)

As soon as food was added, the fish began "tasting" the water by flaring their opercula and swimming rapidly forward for a few seconds. After 1-2 min they began to feed, circuiting the tank and swimming in the same direction at about the same speed. Within each experiment, the mean voluntary swimming speed and the associated respiration rate remained nearly constant throughout the entire 7-h feeding period (Figures 1, 2). The mean swimming speed was established during the first 15 min of feeding and was related to the amount of plankton in the water (Figure 4). Within a range of about 1.5-4 μg chlorophyll *a*/l the voluntary swimming speed and respiration rate of the fish were roughly proportional to the chlorophyll *a* content of the water. Above about 4 μg chlorophyll *a*/l however, the swimming speed was independent of plankton concentration. In the three high-ration experiments during feeding, the mean speed $\pm$95% was 41.3$\pm$1.5 cm/s and the corresponding mean respiration rate was 0.48$\pm$0.029 mg O_2/g per h. The relationship between chlorophyll *a* concentration and the voluntary swimming speed can be described by a rectangular hyperbola [Equation (1), see Figure 4]. The zero point for the curve was taken as the mean swimming speed of unfed fish (12.2 cm/s) and the approximate concentration threshold (1 μg chlorophyll *a*/l) (Durbin and Durbin 1975) of *D. brightwelli* at which Atlantic menhaden will begin to feed.

In these experiments the mean voluntary swimming speed of the Atlantic menhaden during feeding ranged between 29.3 and 43.4 cm/s (1.14-1.68 BL/s). This represented a 2.2-3.3 fold increase over the mean prefeeding routine swimming speed (12.2 cm/s). Respiration rates during feeding ranged between 0.221 and 0.538 mg O_2/g per h and were thus elevated 2.2-5.4 fold over the mean initial routine respiration rate (0.10 mg O_2/g per h). There was a good linear relationship between the mean swimming speed during feeding and the $\log_{10}$ transformed mean respiration rate (Figure 5, Table 2).

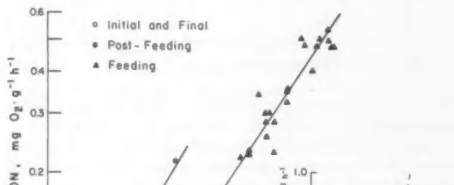

FIGURE 5.—Relationships between mean voluntary swimming speed and mean respiration rate of a school of 12 Atlantic menhaden. The $\bar{x}$ and 95% confidence limits of the initial and final measurements are shown; functional regressions shown for the feeding and postfeeding measurements are presented in Table 2. Inset is an arithmetic plot of Equation (3); extrapolations beyond observed data are dashed.

Postfeeding Measurements (No. 6, 7, 8)

When the input of food was stopped at the end of 7 h, the fish rapidly depleted the plankton remaining in the tank. Within 5 min the swimming speed of the fish decreased noticeably, and as plankton levels continued to decline, the fish progressively reduced their swimming speed (Figure 1, measurement 5). Respiration rates also declined (Figure 2). Feeding usually became intermittent within 15-20 min, and ceased entirely during the next one-half hour, at which time the plankton in the tank had been reduced to a negligible level.

After the Atlantic menhaden had removed the last of the plankton, they continued to "taste" the water fairly frequently and were somewhat restless, as though searching for additional food. During this postfeeding period, however, there was a gradual return toward the prefeeding behavior. Dusk arrived during or shortly after the second postfeeding measurement. Although it was not possible to photograph the fish during the third postfeeding measurement at midnight, their activity levels appeared to be very low as indicated by their low respiration rates, and qualitative observations of their swimming behavior in the dim light.

The postfeeding measurements were spaced too far apart to precisely define the time by which the fish returned to their routine activity and metabolic levels. In general the duration of this

period was greater with larger ration sizes (~4.5 h, experiment 4); at low food levels (e.g., experiments 7, 9) the respiration rate had essentially returned to baseline in <2 h (Figure 2).

The mean swimming speed of the first two postfeeding measurements (no. 6, 7) usually fell within the range of the routine swimming speeds; however, the respiration rates tended to be elevated above the routine rates (Figure 5). There was a linear relationship between mean swimming speed and $\log_{10}$ respiration rate in these postfeeding measurements (Figure 5, Table 2).

DISCUSSION

These results demonstrate that the voluntary swimming speed of adult Atlantic menhaden is related to the availability of plankton food in the water. If food is not present, the voluntary swimming speed and respiratory rate of Atlantic menhaden are low. Swimming speed increases during feeding, following an approximately hyperbolic relationship with increasing plankton density in the water. Over a wide range of plankton concentrations the characteristic swimming speed of the menhaden is about 1.60 BL/s, with a respiratory rate of about 0.48 mg O_2/g per h. This approximately 5-fold increase in respiratory rate above the routine implies that the energy expenditures during feeding will be a major element in the energy budget of menhaden.

Previous descriptions of menhaden feeding behavior (Durbin and Durbin 1975), based on short-term experiments in which the plankton concentration decreased during the course of each experiment, were generally confirmed by the present study. However, respiration rates measured in the present study indicate that the feeding frenzy, which was observed in the earlier study after a large amount of zooplankton was added to the tank, is not likely to persist during prolonged feeding in nature. Swimming speeds during the frenzy were estimated to be about 2-2.5 BL/s. The energy cost of swimming at these speeds, as estimated from Equation 3 (Table 2), would be high (10-23 times the routine metabolic rate) and would not appear to be bioenergetically profitable over prolonged periods.

The same general behavior patterns have been observed in five groups of Atlantic menhaden collected during three summers. Such consistency indicates that the behavior of the Atlantic menhaden in the laboratory can provide insight into their behavior in the field. However, these laboratory based predictions of menhaden swimming speeds need to be tested in the field.

Satiation has often been observed to be an important feature which affects the feeding behavior of fishes (i.e., Ivlev 1961). This is most evident for "macrophageous" fishes (those which take their food in large particles). In the present study, however, there was no evidence of satiation even with the largest ration, when the fish consumed the equivalent of 8% of their body weight during a 7-h period. Evidence of satiation would include a decrease in their swimming speed during the experiments or a switch to intermittent feeding. In contrast, the fish fed continuously at a constant rate as long as food was available, and they continued to search for food after it stopped coming into the tank. Plankton densities sufficient to saturate the physical capacity of menhaden to handle and process food may not be of much ecological significance. This is because natural plankton populations in the size range which can be filtered by menhaden are seldom found in concentrations greater than those used in the present experiments. The high concentrations of chlorophyll *a* which occur in coastal and estuarine waters during the summer are primarily small flagellates (e.g., Durbin et al. 1975), which are too small to be retained on the gill rakers of the menhaden (Durbin and Durbin 1975).

There are comparatively few studies which have simultaneously measured routine respiration rate and activity. At very low swimming speeds, respiration rate has been found to be linearly (Spoor 1946) and log linearly (Smit 1965; Muir et al. 1965) related to activity. In the present study, the routine swimming speeds were clustered within a narrow range (0.36-0.59 BL/s), and there was no detectable relationship between respiration rate and swimming speed.

In all of the nonfeeding (initial, final, postfeeding) measurements, the respiration rates were higher than those which would have been predicted from the observed swimming speeds and an extrapolation of Equation (3) (Table 2, Figure 5). Thus the respiration rates of the fish when they were not feeding, and therefore swimming slowly, were higher per unit swimming speed than when the fish were feeding and swimming more rapidly. These results were consistent with previous studies, in which routine metabolic rates also tended to be variable, and elevated above those

predicted from respiration rate-swimming speed relationships during long-term swimming at constant speed (Brett 1964; Smit 1965; Muir and Niimi 1972). Explanations for this phenomenon include: 1) stress, which elevates the metabolic rate, is reduced when the fish are occupied by some activity such as swimming against a water current (Brett 1964), or feeding, if the fish are nonaggressive (this study); 2) the intermittent swimming of spontaneously active fish, accompanied by frequent accelerations and changes in direction, is hydrodynamically less efficient than the smooth caudal locomotion of continuous swimming and thus exacts a relatively higher metabolic cost (Smit 1965).

The increased respiration rates during feeding consumed a significant fraction of the energy obtained from the ration (Table 1, column 6). Energy expenditures above routine during the postfeeding period averaged 4.61% of the energy contained in the food ration (Table 1, column 9). The increased metabolic rate during and soon after feeding appeared to be primarily due to the increased voluntary swimming speed. Swimming speed accounted for 84.3% of the variability in metabolic rate during feeding and 73.3% during the postfeeding period (Table 2). Other factors which may affect the metabolic rate as a result of feeding include changes in excitability of the fish, and the calorigenic effect of the food ration (SDA, the "specific dynamic affect").

The excitability of the fish is in practice difficult to measure. Qualitative observations of the behavior of the fish and the degree of variability in their swimming behavior (Figure 3) indicated that excitability was not a significant factor contributing to the elevated respiration during feeding, but could be important during the postfeeding period of restlessness. The latter evidently resulted from the abrupt termination of the input of food when the fish were not satiated.

The cost of digestion and transformation of the food, or SDA, has generally been measured as an increase in oxygen consumption following feeding (Kleiber 1961; Warren and Davis 1967). In several earlier studies, in which fish were fed a single meal over a brief period, the increase in oxygen consumption peaked several hours after the meal, then gradually subsided over a prolonged period (as long as 2-3 d) to the prefeeding level (Muir and Niimi 1972; Pierce and Wissing 1974; Beamish 1974). In these species, digestion of the food also occurs over an extended period. The energy loss to SDA was generally estimated to represent about 12-16% of the energy content of the ration.

The Atlantic menhaden results differed considerably from these earlier studies. There was no peak in oxygen consumption during the postfeeding period, but instead a rapid and continuous return of the metabolic rate to the prefeeding level. This rapid return is consistent with the rapid digestion rates observed for menhaden.[4] Food was assimilated within 1-2 h after ingestion, and approximately 80% of the food ingested during the 7-h feeding period was digested and assimilated within the same period. The amount of energy expended above the routine during the postfeeding period was larger in the larger ration experiments (Table 1, columns 7, 8), which may appear to indicate some effect of SDA. However, voluntary activity levels were also higher in these experiments. SDA is believed to be proportional to ration size, but if the oxygen consumption attributable to swimming activity, Equation (3) (Table 2) is subtracted from the total respiration rate during the postfeeding period, there was no relationship between ration size and the amount of elevated respiration which can be ascribed to SDA.

Thus, while Atlantic menhaden may be assumed to experience some respiratory costs related to SDA, the major part of these will be included as a part of the total respiratory increase during feeding. In practice it would be very difficult to distinguish SDA in the total metabolism because of the overwhelming effect of swimming speed on the metabolic rate.

Equations (2) and (3) (Table 2) may be extrapolated to zero activity to obtain an estimate of standard metabolism. These estimates, 0.036 mg O_2/g per h from Equation (2) and 0.029 mg O_2/g per h from Equation (3) are generally lower than those reported from most other fishes which have been studied (Table 3). Respiration rates which menhaden sustained during feeding were also high relative to those which can be sustained by other species, and actually exceeded the active rate (the maximum which can be maintained for 1 h) (Brett 1964) of a number of species, including the aholehole, largemouth bass, rainbow trout, and tilapia (Table 3). Since the present study measured only voluntary respiration rates, the active

[4]Durbin, E. G., and A. G. Durbin. Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden *Brevoortia tyrannus*. Unpubl. manuscr.

TABLE 3.—Metabolic rates among 10 fish species. Except where noted, rates were extrapolated to a 300 g fish, using the appropriate weight-swimming speed-respiration relationships.

Species	Temperature (° C)	Standard mg O_2/g per h	Active mg O_2/g per h	Author
Brook trout, *Salvelinus fontinalis*	20	0.153		Beamish (1964)
White sucker, *Catostomus commersonii*	20	0.056		Beamish (1964)
Brown bullhead, *Ictalurus nebulosus*	20	0.093		Beamish (1964)
Carp, *Cyprinus carpio*	20	0.043		Beamish (1964)
Tilapia, *Tilapia nilotica*	25	0.086	0.378	Farmer and Beamish (1969)
Largemouth bass, *Micropterus salmoides*	20	~0.10	0.302	Beamish (1970)
Rainbow trout, *Salmo gairdneri*[1]	15	0.073	0.48	Webb (1971)
Aholehole, *Kuhlia sandvicensis*	23	0.043	0.387	Muir and Niimi (1972)
Sockeye salmon, *Oncorhynchus nerka*	20	0.103	0.799	Brett and Glass (1973)
Atlantic menhaden, *Brevoortia tyrannus*[1]	20	0.029	(0.538)[2]	This study

[1]Actual measured values; $\bar{x}$ wet weight of rainbow trout = 272 g, and Atlantic menhaden = 302 g.
[2]Maximum voluntary metabolic rate in this study; presumably less than active rate.

rate in menhaden remains unknown, though presumably higher than those reported here. Thus the metabolic "scope" (Fry 1947) in menhaden appears to be significantly larger than that of many species. A large metabolic scope is consistent with Hartwell and Otto's (1978) finding that the critical swimming speeds in juvenile Atlantic menhaden far exceed those reported from other species: at 20° C nonfeeding fish averaging 5.8 cm standard length were able to maintain a speed of 15.8 BL/s for 64 min and a speed of 20.8 BL/s for 2 min. In contrast, at 20° C the critical speed of a 6 cm sockeye salmon, for example, is only about 6.5 BL/s (Brett and Glass 1973).

The respiration during feeding increased significantly faster per increment in swimming speed in menhaden than in other species which have been studied. In Atlantic menhaden an increase in swimming speed of 1 BL/s caused a 5.8-fold increase in the respiration rate (Table 2, Equation (3)); while for eight species reviewed by Beamish (1978) (*Oncorhynchus nerka*, *Lepomis gibbosus*, *Melanogrammus aeglefinus*, *Tilapia nilotica*, *Micropterus salmoides*, *Liza macrolepis*, *Cyprinus carpio*, *Salmo gairdneri*), a similar increase in speed caused a roughly 2.3-fold elevation in the metabolic rate. Thus the cost of increasing the swimming speed is 2.5 times higher in Atlantic menhaden during feeding than in these eight species (which were not feeding).

The very steep slope of the swimming speed-respiration relation for the Atlantic menhaden indicates that during feeding, the loss in streamlining caused by the expanded opercula and the resistance of the closely spaced gill rakers substantially increase the hydrodynamic drag of the fish. It is likely that the respiratory cost for nonfeeding Atlantic menhaden swimming at equivalent speeds would be much lower. It would be of interest to determine the maximum swimming performance of nonfeeding adult fish, for comparison with Hartwell and Otto's (1978) data from juveniles.

The rapidly increasing respiratory cost of swimming during feeding is perhaps more clearly illustrated when the relationship is plotted arithmetically (Figure 5, inset). The highest mean voluntary swimming speed in the present experiments, 43.4 cm/s or 1.68 BL/s, is very close to the inflection of the curve in Figure 5 (inset), beyond which an increase in swimming speed drastically increases the metabolic rate. Because of the high energy cost it is likely that in nature the voluntary swimming speeds of adult Atlantic menhaden during feeding will be <2 BL/s for most of the time.

In conclusion, the Atlantic menhaden, a filter-feeding planktivore, offers an interesting contrast to pelagic predaceous fishes, which have been more widely studied (Durbin 1979). These predators typically consume their daily ration in a few large meals (they are "macrophagists"). The time and energy costs of feeding varies in different species, and the energy lost to SDA is a conspicuous component of their daily metabolism. In contrast, a "microphagist," such as the Atlantic menhaden, consumes its food as a continuous stream of very small food particles. While the energy cost associated with feeding is consistently high, in menhaden there is no extended period of elevated respiration following feeding, as observed in macrophagists, but rather a continuous and rapid return to prefeeding rates.

ACKNOWLEDGMENT

We would like to thank Harold Loftes, skipper of the *Ocean State*, and Charles Follett, skipper of the *Cindy Bett*, for their assistance in obtaining

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USING BOX-JENKINS MODELS TO FORECAST FISHERY DYNAMICS: IDENTIFICATION, ESTIMATION, AND CHECKING

ROY MENDELSSOHN[1]

ABSTRACT

Box-Jenkins models are suggested as appropriate models for forecasting fishery dynamics. Unlike standard production models, these models are empirical, dynamic, stochastic models. Box-Jenkins models are not biased when estimating relationships between catch and effort, as are standard production models. The use of these techniques is illustrated on catch and effort data for the skipjack tuna fleet in Hawaii. An actual 12-month forecast is shown to give a reasonable fit to the observed data. Most of the discrepancies are explained by changes in the behavior of the fishermen (i.e., economic factors), rather than by lack of knowledge of the behavior of fish.

Accurate forecasting models would be useful in fishery management because extended jurisdiction and international agreements require preseasonal predictions of the actual catch of a fleet. In addition, improved forecasts of fish availability can lead to improved planning by fishermen or by processing firms. Forecasting techniques have expanded greatly in the last years, but few have been adapted to research in fisheries management. Instead, techniques designed to establish the equilibrium health of the stocks are also being used to attempt dynamic forecasting.

At present, two least squares procedures are being used to estimate the general production model, the search procedure of Pella and Tomlinson (1969) and the weighted least squares of Fox (1970, 1971, 1975). The Fox procedure fits catch per unit effort against a function of lagged effort. Several authors (Chayes 1949; Eberhardt 1970; Atchley et al. 1976) have demonstrated that scaling the dependent variable (i.e., catch) by the independent variables (i.e., effort) biases the fit by introducing artificial correlation into the data. Johnston (1972) showed that ordinary least squares gave biased estimates and an inflated F-statistic when used with variables lagged on themselves. Neither the Fox nor the Pella-Tomlinson procedure accounts for the effect of autocorrelated errors in the estimation procedure which Granger and Newbold (1977) and Newbold and Davies (1978) have demonstrated bias both estimation and tests of fit. An examination of the residuals in Fox (1971, figure 3B) clearly shows them to be autocorrelated. Residuals from many spawner-recruit curves display similar behavior.

In this paper, the use of Box-Jenkins models for modeling and forecasting fisheries dynamics is explored. Box-Jenkins and other related forecasting techniques are specifically designed for estimating and testing models in the presence of autocorrelated errors. The fitted models are stochastic rather than deterministic, thus reflecting the variability found in most fisheries. The models are constructed empirically, and are best suited for forecasting. The models tell us little about the long-term health of the stocks, so that a judicious use of production, yield per recruit, and accurate forecasting models is required to give the best overall picture of the fishery.

My preference for Box-Jenkins models over other forecasting methods now available is due to the good documentation (see for example Anderson 1975; Box and Jenkins 1976; Granger and Newbold 1977) and computer accessibility. The results presented here were obtained using a package originally developed by David Pack at Ohio State University and now available through Automatic Forecasting Systems.[2]

The three-step process of model identification, model estimation, and model diagnostic checking is illustrated by developing a model that makes monthly forecasts of skipjack tuna, *Katsuwonus pelamis*, catches in Hawaii. Experience with the model suggests that for a 12-mo forecast of catch,

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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during peak months the forecast is within 15% of the observed catch (and is usually within 8-10% of the observed catch), most turning points in the catch trend are predicted, and the important feature of a low, flat catch during the summer months or high, peaked catches are accurately predicted. Moreover, the reasons for forecasts with large errors appear to be related more to fishermen's decisions in face of weather and economic factors, than to mispredicting the availability of the fish.

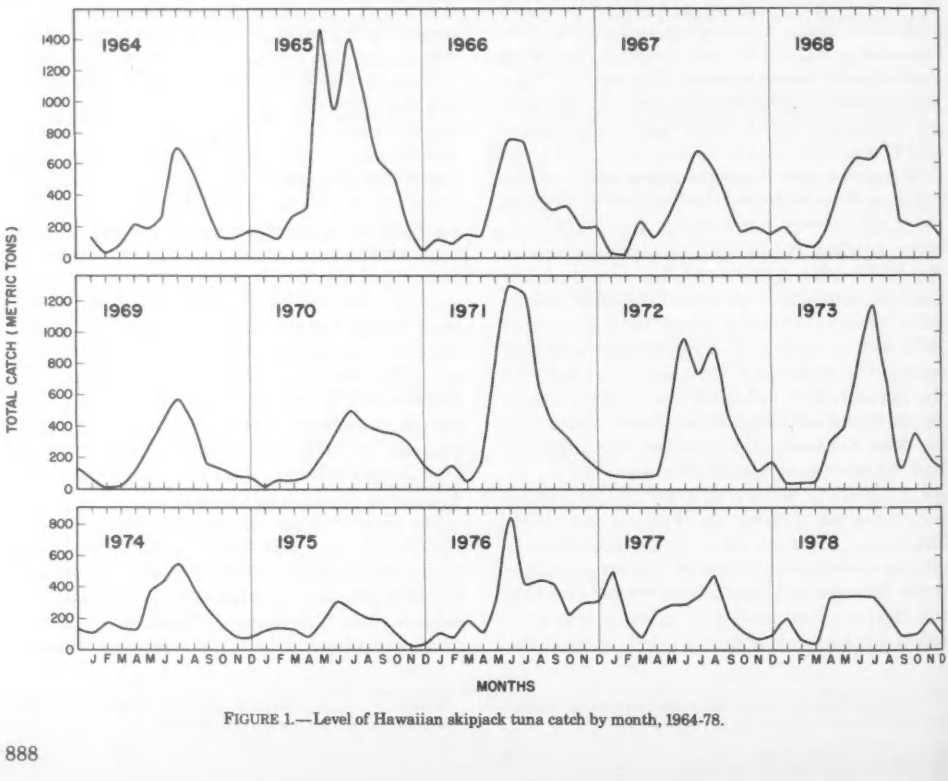
THE DATA AND UNDERLYING MODEL

The data to be analyzed are landings of skipjack tuna by approximately 12 boats from Oahu during 1964 through 1978. The raw data consist of the daily landings (each boat rarely stayed out more than a day or two), broken down by boat, and by four skipjack tuna size classes: large, medium, small, and extra small. For purposes of analysis, the data were aggregated into monthly totals, with the total number of fishing trips used as the measure of fishing effort. For monthly catch and effort during 1964-78 see Figures 1 and 2.

There are several causes for the observed seasonal variability. First, the tuna are only available in large numbers seasonally. Second, price considerations, particularly around Christmas and New Year when there is large demand, tend to spur fishing even when availability is low. Third, with only 12 boats fishing, if 1 or 2 boats are not able to fish for a few weeks, the catch will drop sharply. Finally, environmental factors, particularly weather (such as bad seas) will affect the landings since the boats are unable to fish.

Folklore in Hawaii has it that the catch remains similar each year, no matter how many boats fish. Comitini[3] examined the fishery using dummy variables and ordinary least squares to estimate

[3]Comitini, S. 1977. An economic analysis of the state of the Hawaiian skipjack tuna fishery. Sea Grant Tech. Rep. UNIHI-SEAGRANT-TR-78-01, 46 p.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MONTHS

FIGURE 1.—Level of Hawaiian skipjack tuna catch by month, 1964-78.

a Cobbs-Douglas production function. He concluded, among other things, that natural fluctuations in resource availablity are significant, but did not include them in his analysis, nor did he provide a means for forecasting future catch. The National Marine Fisheries Service, using a regression model based on the previous year's catch, water temperature, and salinity at the start of the year, makes yearly predictions that have been mixed in accuracy.

Box-Jenkins models are autoregressive-integrated-moving-average models, or ARIMA models. These are linear, stochastic models that can describe fairly complex behavior, in contrast to Parrish and MacCall (1978) who use highly nonlinear equations to model the fluctuations in fishery data.

The modeling is based on the properties of stationary time series. A time series x_t is stationary if it has a constant mean, and if the covariance between events x_t, x_{t-s} depends only on s and not on t. Many series are stationary after removing a deterministic trend. Others are differenced in order to achieve stationary. Also, transforming the time series, particularly using the Box-Cox family of transformations, often improves the behavior of the time series. The initial step then is to transform and difference the data as necessary to achieve stationary. It is convenient to use the backshift operator B^j, where $B^j x_t = x_{t-j}$, to denote lagged variables. Given the new series $z_t = (1 - B^d)x_t$, a mixture of autoregressive and moving average models are sought. Autoregressive models are models that depend on the past history of the time series:

$$z_t = \phi_1 z_{t-1} + \phi_2 z_{t-2} + \ldots + \phi_p z_{t-p} + a_t$$

in terms of the backshift operator:

$$(1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p) z_t = a_t$$

while moving average models depend on past values of the noise or error:

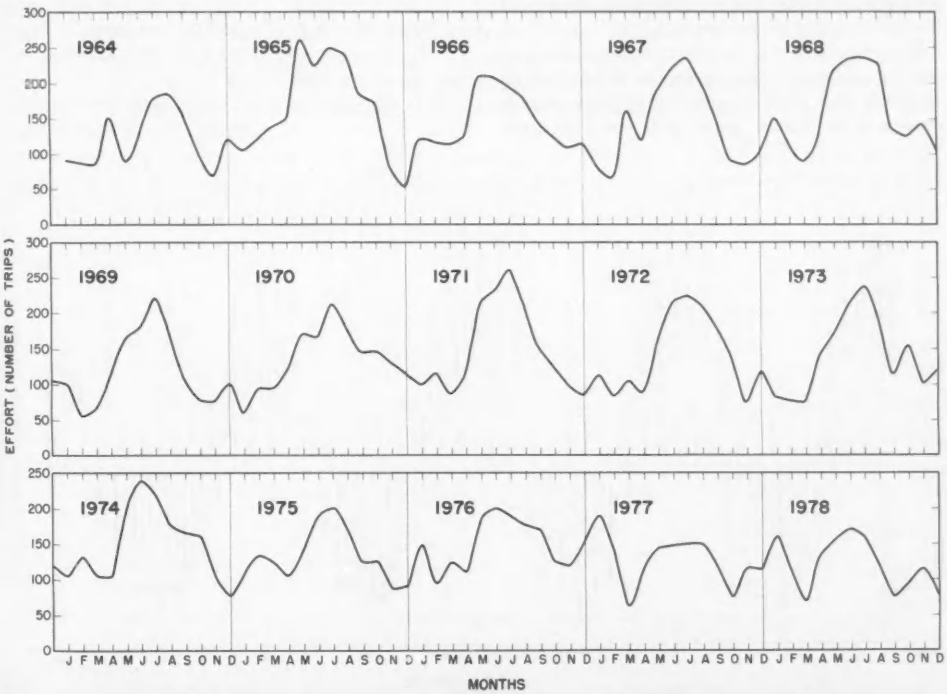

FIGURE 2.—Number of fishing trips per month by the Hawaii skipjack tuna fleet 1964-78, near Oahu, Hawaii.

$$z_t = a_t - \theta_1 a_{t-1} - \theta_2 a_{t-2} - \ldots - \theta_q a_{t-q}$$

or:

$$z_t = (1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q) a_t.$$

A model that has both moving average and autoregressive parameters is a mixed autoregressive moving average model, whose representation in terms of the backshift operator is:

$$(1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p)(1 - B)^d x_t$$

$$= (1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q) a_t.$$

MODEL IDENTIFICATION

The first step in the Box-Jenkins modeling process is to use properties of the data to tentatively identify a model. Even if a multivariate model (i.e., a model based on catch and effort) is the ultimate goal, univariate models of each series are constructed first. Often the univariate model produces forecasts that are almost as accurate as the multivariate model forecast.

My procedure was to identify, estimate, and check a series of models based on the data from January 1964 through July 1977. These models were used to forecast the already observed catch and effort for the period August 1977-December 1978. The models with the best "fit" were then reestimated to make the forecast for 1979. To make clear the feedback nature of identification, estimation, and checking in Box-Jenkins models, results from models fixed to 163 and 180 mo of data are intermingled, but clearly labeled.

A tentative model can be identified by estimating the autocorrelation and partial autocorrelation functions for each series. These are shown in Figures 3 and 4. Significant is the undamped sinusoidal behavior of each, with a period of 12 mo. Failure of both the autocorrelation and partial autocorrelation functions to go to zero is a sign of a nonstationary series, and the need for differencing. The 12-mo period suggested a yearly seasonal model, so that twelfth differences were taken, i.e., $z_t = (1 - B^{12}) x_t$.

The estimated autocorrelation and partial autocorrelation functions for the differenced catch and effort series are given in Tables 1 and 2. Following guidelines in appendix 9.1 in Box and Jenkins (1976), seasonal models with period s of the form:

$$z_t = (1 - \theta_1 B - \theta_2 B^2)(1 - \Theta_1 B^s) a_t \quad \text{(1a)}$$

or $$z_t = (1 - \theta_1 B - \theta_2 B^2)$$

$$(1 - \Theta_1 B^s - \Theta_2 B^{2s}) a_t \quad \text{(1b)}$$

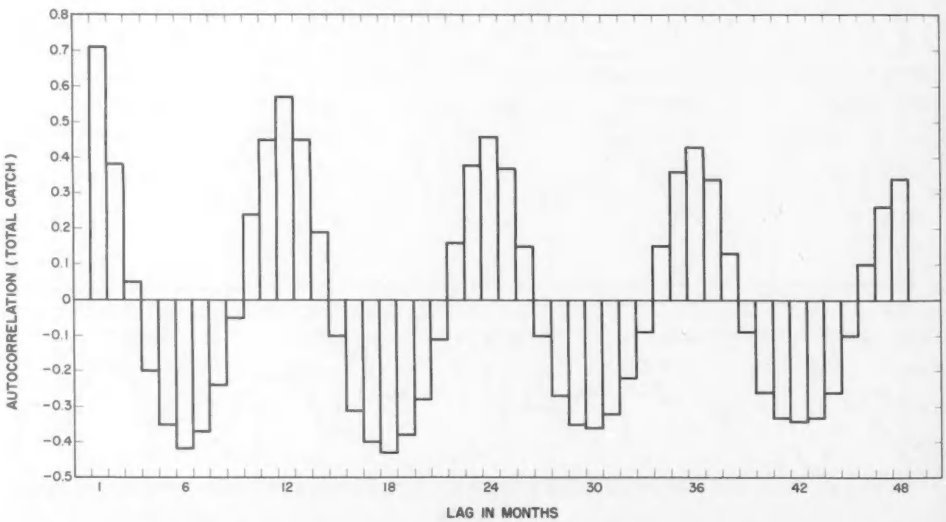

FIGURE 3.—Estimated total catch autocorrelation function for the catch of skipjack tuna near Oahu, Hawaii, 1964-78.

TABLE 1.—Autocorrelation functions for 12th differenced effort series of the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Regular auto.	0.39	0.17	0.20	0.16	0.10	0.04	0.03	0.07	−0.02	−0.08	−0.20	−0.45	−0.18	−0.08
SE	.08	.09	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10	.12	.12
Partial auto.	.39	.03	.15	.03	.01	−.04	.00	.00	−.08	−.07	−.19	−.39	.15	.04

Item	Lag (mo) 15	16	17	18	19	20	21	22	23	24	25	26	27
Regular auto.	−0.18	−0.13	−0.12	−0.17	−0.15	−0.17	−0.12	0.05	0.04	0.02	0.00	−0.07	0.03
SE	.12	.12	.12	.12	.12	.12	.13	.13	.13	.13	.13	.13	.13
Partial auto.	−.03	.02	−.07	−.14	−.01	−.02	−.05	.16	−.08	−.19	.05	−.12	.03

TABLE 2.—Autocorrelation functions for 12th differenced catch series of the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Regular auto.	0.58	0.40	0.33	0.20	0.11	0.05	0.01	0.02	−0.06	−0.12	−0.21	−0.38	−0.21	−0.15
SE	.08	.11	.12	.12	.12	.12	.12	.12	.12	.12	.13	.13	.14	.14
Partial auto.	.58	.09	.10	−.07	−.03	−.04	−.00	.04	−.11	−.07	−.17	−.29	.28	.03

Item	Lag (mo) 15	16	17	18	19	20	21	22	23	24	25	26	27
Regular auto.	−0.16	−0.12	−0.08	−0.09	−0.08	−0.12	−0.10	−0.08	−0.08	−0.09	−0.06	−0.06	−0.05
SE	.14	.14	.14	.14	.14	.14	.14	.14	.14	.14	.14	.14	.14
Partial auto.	−.01	−.06	−.02	−.07	.02	−.05	−.04	−.04	−.11	−.17	−.19	−.01	−.02

were hypothesized as the appropriate univariate models for both the catch and the effort time series.

ESTIMATION AND CHECKING

Given a tentative model, such as Model (1), the next step is a recursive procedure of estimating the parameters of the model, calculating the autocorrelation and partial autocorrelation functions of the residuals from the estimated model, and then testing the residuals for significant departure from the assumption that they are white noise. When a final model has been identi-

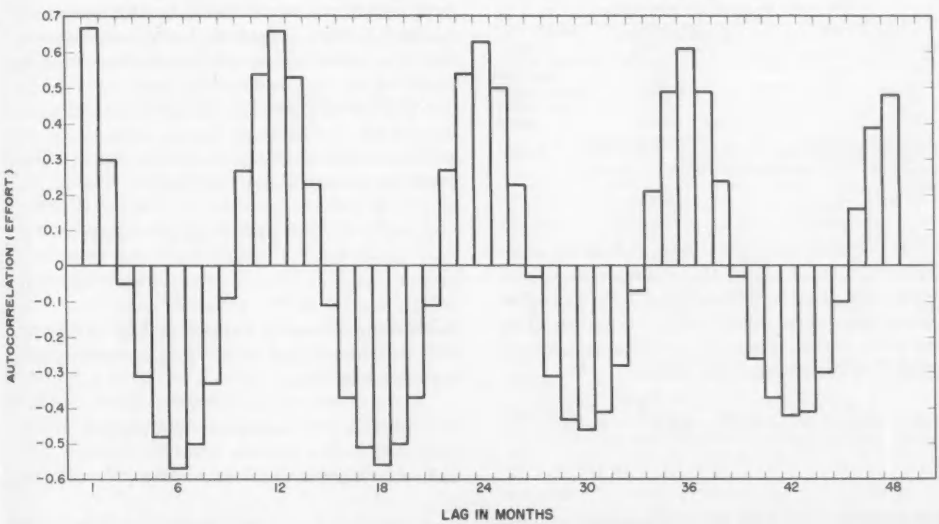

FIGURE 4.—Estimated effort autocorrelation function for the fishing trips by the Hawaii skipjack tuna fleet near Oahu, Hawaii, 1964-78.

fied, overfitting is tried, that is extra parameters are added to see if they are found to be not significantly different from zero.

To insure that I found the simplest model possible, I fitted first the model $z_t = (1 - \theta_1 B)(1 - \Theta_1 B^{12})a_t$, and then added parameters as seemed necessary based on the diagnostic checking. The estimates for Model (1) for catch and effort are given in Tables 3 and 4. Estimates using two estimation techniques, one using backforecasting and one suppressing it, are presented. Some programs do not have a backforecasting feature; my experience is that the estimated models obtained using backforecasting are far superior, as can be seen in the tables presented.

TABLE 3.—Parameter estimates for effort model, Model (1) (see text). (Based on 180 observations.)

Parameter	Estimate supressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.38349	0.07942	−0.44756	0.07886
θ_2	−.11326	.07996	−.12795	.07911
Θ_1	.5894	.08122	.99493	.00650
Θ_2	.00069	.08609	—	—
χ^2 statistic on residuals	26.894 with 44 df		37.319 with 45 df	
Residual mean square	1,018.60		755.270	
Residual SE	31.915		27.482	
Residual mean	1.629		0.5338	

TABLE 4.—Parameter estimates for catch model, Model (1) (see text). (Based on 163 observations.)

Parameter	Estimate suppressing backforecasting	SE
θ_1	−0.54100	0.08190
θ_2	−.22745	.08235
Θ_1	.75314	.08718
Θ_2	.05184	.09256
χ^2 statistic on residuals	27.470 with 43 df	
Residual mean square	165,410	
Residual SE	406.71	
Residual mean	17.506	

The estimated autocorrelation and partial autocorrelation functions of the residuals from both models are given in Tables 5 and 6. For the effort series, there is no sign of a lack of fit, while for the catch series terms of lag three or four are suggested. An overspecified model:

$$z_t = (1 - \theta_1 B^1 - \theta_2 B^2 - \theta_3 B^3 - \theta_4 B^4)(1 - \Theta_1 B^{12})a_t \quad (2)$$

was estimated for both the catch and effort time series. The results are summarized in Tables 7 and 8. The estimated autocorrelation and partial autocorrelation functions of the residuals (not shown) show no sign of additional lags or trend. The test statistic that the residual series are not significantly different from white noise gave no reason to doubt the models adequacy, and overfitting by including a $\Theta_2 B^{24}$ term found this term to be nonsignificant.

TRANSFER FUNCTION MODELS

If both the catch time series, say y_t, and the effort time series, say x_t, have been suitably transformed so that the resulting series are stationary, a transfer function of the form:

$$(1 - \delta_1 B - \delta_2 B^2 - \ldots - \delta_r B^r)x_t = (\omega_0 - \omega_1 B - \omega_2 B^2 - \ldots - \omega_s B^s)y_{t-b} + \eta_t$$

can be estimated where η_t is not assumed to be white noise, but itself can be modeled as an autoregressive-moving average process of a_t.

The procedures for identifying and estimating a transfer function model are similar to those for the univariate model, except that attention is focused on the estimated cross-correlation function between the "prewhitened" catch and effort series. Series are prewhitened if they are reduced to the residuals left from a given model. In this instance, both series are prewhitened by the univariate model for effort estimated in the preceding section. The estimated correlation function, impulse response function, and residual noise autocorrelation function are given in Table 9. The estimated autocorrelation function for the noise is similar to the original univariate autocorrelations, suggesting a noise model of the form:

$$\eta_t = (1 - \theta_1 B - \theta_2 B^2 - \theta_3 B^3 - \theta_4 B^4)(1 - \Theta_1 B^{12})a_t. \quad (3)$$

Based on guidelines in Box and Jenkins (1976:386-388) and knowledge of the fishery, two models were hypothesized:

$$(1 - B^{12})y_t = (\omega_0)(1 - B^{12})x_t + \eta_t \quad (4)$$

and:

$$(1 - \delta_1 B - \delta_2 B^2)(1 - B^{12})y_t = (\omega_0 - \omega_1 B - \omega_2 B^2)(1 - B^{12})x_t + \eta_t. \quad (5)$$

Tables 10 and 11 summarize the estimates when

TABLE 5.—Estimated autocorrelation function for residuals of effort model for the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12
Auto.	0.01	0.03	0.09	0.06	0.04	−0.11	−0.05	0.04	−0.09	0.02	0.03	−0.01
SE	.07	.07	.07	.08	.08	.08	.08	.08	.08	.08	.08	.08
Item	Lag (mo) 13	14	15	16	17	18	19	20	21	22	23	24
Auto.	0.05	−0.01	−0.04	−0.09	−0.08	−0.09	−0.07	−0.08	−0.16	0.10	0.07	−0.02
SE	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08

TABLE 6.—Estimated autocorrelation function for residuals of catch model for the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12
Auto.	0.04	0.11	0.23	0.06	0.06	−0.05	0.00	0.10	−0.03	0.04	0.01	0.00
SE	.08	.08	.08	.09	.09	.09	.09	.09	.09	.09	.09	.09
Item	Lag (mo) 13	14	15	16	17	18	19	20	21	22	23	24
Auto.	0.05	−0.01	−0.07	−0.01	−0.00	−0.04	0.00	−0.01	−0.06	0.01	−0.04	−0.03
SE	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09

backforecasting is used in estimating the parameters for Models (4) and (5). The chi-square statistics show no reason to suspect model inadequacy. The residuals show no significant cross-correlation with total catch, when $1/\sqrt{180}$ (180 observations in the series) is used as a rough standard error. The residual autocorrelation function shows spikes around lag 15 that are higher than would be desired, but overall the fit is reasonable, and the model residuals could reasonably be modeled as white noise.

TABLE 7.—Parameter estimates for effort model, Model (2) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.36746	0.08004	−0.43862	0.07930
θ_2	−.14976	.08412	−.18144	.08590
θ_3	−.16111	.08458	−.15377	.08617
θ_4	−.17096	.08454	−.16298	.08593
θ_5	−.11547	.08089	−.17291	.07998
Θ_1	.59065	.06431	.99483	.00033
χ^2 statistic on residuals	20.696 with 42 df		27.494 with 42 df	
Residual mean square	1,000.40		752.67	
Residual SE	31.629		27.435	
Residual mean	.82151		.35175	

TABLE 8.—Parameter estimates for catch model, Model (2) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.55368	0.07972	−0.53771	0.07462
θ_2	−.35882	.08989	−.43825	.07543
θ_3	−.33817	.09056	−.41197	.01144
θ_4	−.24282	.09012	−.30909	.07479
θ_5	−.12294	.07994	−.14974	.07440
Θ_1	.76951	.05062	.99585	.00825
χ^2 statistic on residuals	15.092 with 42 df		20.384 with 42 df	
Residual mean square	143,240		115,170	
Residual SE	378.47		339.37	
Residual mean	2.1150		3.3299	

DISCUSSION AND FORECASTS

Two transfer function models and one univariate model have been used to forecast the catch and effort in the skipjack tuna fishery during 1979. It is worth emphasizing that the original 12-mo forecasts were made in January 1979 and the updated forecasts were made in May 1979, so the reported results are true forecasts—there was no a priori knowledge of the data to help improve the "fit" of the forecasts. The original catch and effort forecasts are given in Tables 12 and 13 while the updated catch forecasts are given in Table 14.

The models used to produce the forecasts are best understood when written out in difference equation form. The univariate model for catch is:

$$y_t = y_{t-12} + (a_t + 0.538a_{t-1} + 0.438a_{t-2} + 0.412a_{t-3} + 0.309a_{t-4}) \quad (6)$$

$$- (0.996a_{t-12} + 0.535a_{t-13} + 0.436a_{t-14} + 0.410a_{t-15} + 0.308a_{t-16}),$$

i.e., catch this month is equal to the catch during the same month last year, adjusted by a difference of the weighted sums of the forecasting errors over the previous 4 mo. If the forecasts this year have consistently underpredicted compared with last year's forecasts, then the estimated catch is increased, while if the forecasts this year have consistently overpredicted compared with last year's forecasts, then the estimated catch is decreased. The forecast maintains a balance between keeping the catch in equilibrium and keeping the error in equilibrium.

This impression of a yearly cycle with variability is reinforced when examining the polynomial

TABLE 9.—Estimated cross-correlation function, impulse response function, and noise autocovariance function for a catch-effort transfer model for the Hawaii skipjack tuna fleet, 1964-78.

Lag (mo)	Estimated cross-correlation	Estimated noise autocovariance	SE	Estimated impulse response weights
0	0.651	—		8.409
1	.080	0.49	0.10	1.035
2	.070	.21	.12	.903
3	.086	.16	.12	1.111
4	−.033	.16	.13	−.431
5	.044	.10	.13	.566
6	−.098	.07	.13	−1.269
7	.099	.03	.13	1.276
8	.103	.13	.13	1.334
9	−.017	.14	.13	−.215
10	.043	−.05	.13	.556
11	−.040	−.14	.13	−.517
12	−.20	−.26	.13	−1.555
13	.026	−.05	.14	.338
14	−.109	.05	.14	−1.404
15	.003	−.12	.14	−.038
16	−.098	−.16	.14	−.415
17	.014	−.01	.14	.043
18	−.110	−.05	.14	−1.271
19	−.037	−.12	.14	.185
20	.006	−.12	.14	−1.422
21	−.006	−.16	.14	−.475
22	−.108	−.11	.14	.080
23	.012	−.18	.15	−.075
24	−.108	−.21	.15	−1.393
25	−.001	−.09	.15	.181
26	−.108	−.08	.15	−1.390

TABLE 10.—Parameter estimates for transfer model, Model (4) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
ω_0	7.5989	0.69403	8.0003	0.83561
θ_1	−.47621	.07993	−.48894	.07851
θ_2	−.32874	.08734	−.32633	.08541
θ_3	−.17034	.08803	−.14853	.08666
θ_4	−.20033	.07905	−.17506	.07822
Θ_1	.83384	.05271	.99587	.00707
χ^2 statistic on residuals	34.953 with 43 df		32.018 with 43 df	
Residual mean square	83,323		71,300	
Residual SE	288.66		267.02	
Residual mean	−15.152		0.18650	

TABLE 11.—Parameter estimates for transfer model, Model (5) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
δ_1	0.01286	0.30389	0.86672	0.22308
δ_2	.88121	.28641	−.70763	.21659
ω_0	7.3488	.73352	8.1855	.82832
ω_1	−1.3011	2.16847	6.7421	1.71214
ω_2	6.8509	2.34577	−7.3133	1.58459
θ_1	−.49924	.08302	−.46980	.08013
θ_2	−.29495	.09102	−.33234	.08870
θ_3	−.16384	.09191	−.17199	.09012
θ_4	−.13639	.08352	−.21746	.08098
Θ_1	.83311	.05511	.99543	.00623
χ^2 statistic on residuals	33.067 with 43 df		38.906 with 43 df	
Residual mean square	85,673		69,066	
Residual SE	292.70		262.80	
Residual mean	−1.9979		−2.4666	

TABLE 12.—Catch forecasts for 1979 for the Hawaii skipjack tuna fleet from Models (1), (4), and (5) (see text).

Month	Model (4)	Model (5)	Model (1)	Observed catch
Jan.	102.24	157.48	159.97	52.6488
Feb.	78.91	123.32	117.81	74.1184
Mar.	121.86	118.83	108.40	102.4088
Apr.	202.05	169.75	175.82	131.0658
May	423.40	406.87	423.95	470.5450
June	595.39	605.68	598.17	358.5100
July	666.16	684.99	607.07	600.6930
Aug.	528.09	535.73	523.14	600.5200
Sept.	297.96	294.92	291.97	148.3070
Oct.	224.28	216.64	222.96	79.3380
Nov.	173.99	168.83	172.94	27.5084
Dec.	133.22	131.61	132.58	84.7755
Total	3,547.55	3,614.65	3,534.78	2,730.4367

TABLE 13.—Predicted and observed number of fishing trips for the Hawaii skipjack tuna fleet in 1979.

Month	Original prediction	Updated prediction	Observed
Jan.	98.93		53
Feb.	97.50		75
Mar.	101.06		78
Apr.	122.30		118
May	174.00	167.71	173
June	196.16	187.36	182
July	209.37	206.14	200
Aug.	183.04	179.81	174
Sept.	139.18	138.73	84
Oct.	121.20	120.45	84
Nov.	104.23	104.83	51
Dec.	100.92	100.51	109

TABLE 14.—Updated forecasts of total catch for 1979 for the Hawaii skipjack tuna fleet.

Month	Model (4)	Model (5)	Model (1)	Observed catch
May	393.214	382.430	401.874	470.545
June	547.014	586.400	589.524	358.510
July	644.638	705.137	668.895	600.693
Aug.	500.151	527.945	521.456	600.520
Sept.	293.130	283.067	289.516	148.307
Oct.	220.557	197.953	222.806	79.336
Nov.	174.567	164.720	173.594	27.5084
Dec.	130.947	136.831	133.148	84.7755
Total	2,904.218	2,984.483	3,000.813	2,370.1949

representation of Model (1). The value of Θ_1 is nearly one. Thus the term $(1 - B^{12})$ appears on both sides of the equation, and can be cancelled. Abraham and Box (1978) showed that this is sufficient reason to suspect a deterministic cosine function trend with a moving average model around the trend. Given the high residual mean square for the model (115, 170), this latter interpretation is consistent with the folklore on the fishery—highly variable but on the average things are similar from year to year.

The first transfer function model is:

$$y_t = 8.003x_t + (y_{t-12} - 8.003x_{t-12}) + (a_t + 0.489a_{t-1} + 0.326a_{t-2} + 0.149a_{t-3} + 0.175a_{t-4}) \quad (7)$$
$$- (0.996a_{t-12} + 0.487a_{t-13} + 0.325a_{t-14} + 0.148a_{t-15} + 0.174a_{t-16}).$$

This model has an interpretation similar to that of the univariate model, except now catch per weighted units of effort are compared between years. The second transfer function model compares lagged values of catch and effort also.

It is difficult to judge the value of a forecast, since this will depend on the use being made of the forecast and the alternatives available. Granger and Newbold (1977) suggested the most appropriate measure of the value of a forecast is a loss function which reflects the loss from inaccurate forecast in the actual application for which the forecasts were developed. For forecasting the skipjack tuna fishery in Hawaii, there were four immediate goals. The first was to give a reasonably accurate estimate of total catch over the year, within a 15-20% error rate. The second was to predict what kind of summer it would be, May through September being the main fishing months. This means predicting what month the fish start running, what month the fish stop running, and whether the catch is high and peaked as in 1979, or flat and low as in 1978. An important concern is the relative size of the drop in catch when it occurs in September or October.

A third concern was an accurate forecast of the catch in December, when the holiday demand for sashimi (a Japanese raw fish delicacy) drives prices very high. And finally, an increased understanding of the dynamics of the fishery was desired.

Based on these criteria, I feel the forecasts have performed well, especially compared with any alternative available. The error in predicting the 1979 total catch is higher than desired. However, for the last 6 mo of 1977 the model forecasted within 8% of the observed total catch, and for the period July 1977-December 1978 the model forecasted within 12% of the observed total catch.

Except for June 1979, the summer months were predicted accurately. Experience with the model on the data from July 1977 suggests that the summer months are almost always predicted within 10% of the observed catch. In fact, in March 1979, an industry representative doubted the high catch forecasted for the summer, due to the low catch in January and February 1979. Similarly, the sharp drop in catch in September was predicted by the model. Again, in August 1979 an industry representative doubted that a sharp decline in catch would occur in September, but said that this could be a useful piece of knowledge since their decisions would change if they knew they could expect the supply to drop sharply.

The forecasts have provided insight into the fishery. The major failures of the forecasts were January 1979 and October-December 1979. January 1979 was a period of unusually bad storms, so that few fishing trips were made. However, the observed catch per trip was 0.993 metric tons (t), while Model (4) predicted a catch per trip of 1.033 t. The main source of the error in the forecast was the predicted number of trips to be made.

Similarly, the high summer catches, coupled with very high catches of yellowfin tuna, drove the price for skipjack tuna to very low levels. At the end of September, most of the boats went into drydock because of the prevailing low prices. The few boats that remained tended not to be the industry leaders (i.e., boats with a proven record of higher catch rates), and made only short forays rather than their usual fishing trips.

The point of these explanations is that the causes of the poor forecasts appear to be related not to the behavior of the fish stocks but rather to the behavior of the fishermen. Therefore, the effort to improve the forecasts needs to be directed at understanding the fishery, rather than the fish. (An economic study of the industry is near completion.)

Finally, water temperature and salinity data for one location off Oahu were included in the transfer function models. These variables added little to the forecasts, and since there is no

mechanistic explanation as to why these variables should affect the catch and effort, they are not being used at this time in the forecasts. (However, the ability to include random environmental factors into the forecasting model is an advantage when using stochastic models as compared with the normal deterministic production models.) Disaggregating by size class might also improve the forecasts. Prior to 1973, the catch of the large skipjack tuna and the total catch were highly correlated. Since 1973, this has not been true and there has been a definite change in the size composition of the catch. A disaggregated intervention model may be able to explain this change.

SUMMARY

Box-Jenkins models have been proposed as an alternate model for forecasting fishery data. ARIMA models provide maximum likelihood estimators that are not biased when the data is seasonal and autocorrelated, and when a variable is lagged on itself. Techniques are explored which allow the model to be constructed from the data up, rather than from theoretical models that may not be supported by the data. The procedure is illustrated on skipjack tuna catches in Hawaii, which traditionally has been considered too variable to forecast on a monthly basis in a reasonable manner.

ACKNOWLEDGMENTS

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DEVELOPMENT OF LARVAL SMOOTH FLOUNDER, *LIOPSETTA PUTNAMI*, WITH A REDESCRIPTION OF DEVELOPMENT OF WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS* (FAMILY PLEURONECTIDAE)[1]

WAYNE A. LAROCHE[2]

ABSTRACT

Larval development is described for the first time for *Liopsetta putnami* and redescribed for *Pseudopleuronectes americanus* (Pleuronectidae). These species cooccur as larvae in Gulf of Maine estuaries during the spring and have previously been difficult to separate, especially as small larvae, due to their similar development and the lack of adequate published descriptions. Characters which distinguish *L. putnami* from *P. americanus* larvae include: presence of darkly pigmented eyes in yolk-sac larvae; lack of internal melanophores over the notochord in larvae greater than 3.2 mm; lack of melanophores on the fins of yolk-sac, preflexion, and flexion larvae; and higher ratio of snout to anus length/standard length (averages 43.6 and 41.2% standard length for yolk-sac and preflexion larvae versus 33.3 and 37.6% standard length for yolk-sac and preflexion larval *P. americanus*).

The smooth flounder, *Liopsetta putnami* (Gill), Family Pleuronectidae, occurs in the western North Atlantic Ocean from Ungava Bay, Quebec, to Providence, R.I. It is found chiefly over muddy bottoms in estuaries and nearshore, marine waters <10 m deep (Bigelow and Schroeder 1953; Leim and Scott 1966). The winter flounder, *Pseudopleuronectes americanus* (Walbaum), Family Pleuronectidae, occurs from Battle Harbour and Windy Tickle, Labrador (lat. 55°45′ N), to Georgia. It is caught over hard bottoms to depths of ≈142 m on the offshore fishing banks and also in estuaries and nearshore, marine waters (Bigelow and Schroeder 1953; Leim and Scott 1966). From Providence, R.I., northwards, *L. putnami* and *P. americanus* cooccur in shallow coastal and estuarine waters where both are known to spawn (Bigelow and Schroeder 1953).

Previously, two large larvae and one small juvenile *L. putnami* have been illustrated and described (Laszlo 1972), while larval and juvenile *P. americanus* have been illustrated and their development briefly described in various publications (Sullivan 1915; Breder 1923; Bigelow and Welsh 1925; Bigelow and Schroeder 1953; Scotton et al. 1973; Lippson and Moran 1974; Klein-MacPhee 1978; Martin and Drewry 1978; and others). However, existing descriptions of *P. americanus* do not accurately present all characters necessary for reliable separation of small larvae when the species cooccur.

This paper describes the larval development of *L. putnami* for the first time from reared and field-collected specimens, redescribes the larval development of *P. americanus*, and compares the two.

METHODS

Two ripe female and one ripe male *L. putnami* were collected from the cooling water intake screens of the Maine Yankee Atomic Power Plant located on Montsweag Bay, Wiscasset, Maine, on 7 February 1974. Most *L. putnami* collected on that date were spent. The ripe fish were artificially spawned, and the eggs were fertilized in the field. Eggs were kept at 5° C in darkened containers of gently aerated 23‰ salinity water, conditions approximating those at the capture site. Field-collected larvae were captured in February and March and also were reared in the laboratory. Larvae were fed field-collected plankton.

Larvae of both *L. putnami* and *P. americanus* were collected and preserved in 3-5% Formalin[3] during 1972, 1973, and 1974 from the Sheepscot

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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and Damariscotta River estuary systems. Larvae were collected with meter nets, ½ m buoyed and anchored nets, and a small beam trawl. The smallest *L. putnami* larvae (3.1 and 3.6 mm) were hatched from the artificially spawned eggs. The 7.1 and 7.6 mm specimens were field collected as small larvae and reared in the laboratory. All other specimens in the series were field collected and preserved. The *P. americanus* series includes only field-collected specimens.

Some specimens were lightly stained with alizarin to facilitate counting of body parts. Illustrations were prepared using a camera lucida. Measurements were taken on the right side of each specimen with an ocular micrometer mounted in a dissecting microscope. Measurements taken include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Total length (TL) = snout tip to tip of caudal fin membrane or fin rays.

Snout to anus length = horizontal distance from snout tip to a vertical through posterior margin of large intestine at anus.

Head length (HL) = snout tip to posterior margin of otic capsule until cleithrum becomes visible (5.4 mm in *L. putnami* vs. 3.7 mm in *P. americanus*), then to the cleithrum; to the posterior margin of the operculum on postflexion larvae >7.0 mm of both species.

Snout length = snout tip to anterior margin of orbit of right eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest width of right eye.

Body depth at pectoral fin base = vertical distance across body at pectoral fin base, not including depth of dorsal fin pterygiophores.

Maximum body depth at pectoral fin base = vertical distance across body at pectoral fin base including depth of dorsal fin pterygiophores.

Body depth behind anus = vertical distance across body immediately posterior to anus, not including depth of dorsal fin pterygiophores.

Maximum body depth behind anus = vertical distance across body immediately posterior to anus including depth of dorsal fin pterygiophores.

Pectoral fin length = distance from base to tip of fin fold or longest fin ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic fin length = distance from insertion of pelvic fin to tip of fin fold or longest ray.

Vertebral and fin ray counts were made on juveniles with the aid of radiographs. All length measurements are standard length unless otherwise stated.

TERMINOLOGY

Yolk-sac larva = prior to absorption of yolk material.

Preflexion larva = prior to notochord flexion.

Flexion larva = undergoing notochord flexion from time urostyle begins to slant upward until urostyle is in final upturned position and caudal fin is formed.

Postflexion larva = from alignment of urostyle in final upturned position and caudal fin formation until attainment of adult dorsal and anal fin complements.

Transforming larva = from onset of migration of left eye, development of juvenile pigment pattern, and change in behavior from pelagic swimming to benthic habit until completion of these processes and attainment of adult pelvic and pectoral fin ray complements.

IDENTIFICATION

Liopsetta putnami and *P. americanus* are the only Gulf of Maine flatfishes that commonly are found in estuaries and that spawn during late winter-early spring (Bigelow and Schroeder 1953). American plaice, *Hippoglossoides platessoides*, and Atlantic halibut, *Hippoglossus hippoglossus*, also spawn during late winter-early spring but rarely enter Gulf of Maine estuaries (Bigelow and Schroeder 1953). Larval *Hippoglossoides platessoides* were described by Bigelow and Schroeder (1953) and have three vertical bands of melanistic pigment across the postanal region. Martin and Drewry (1978) compiled and summarized descriptions of larval *Hippoglossus hippoglossus* which lack vertical bands of melanistic pigment across the postanal region and hatch at lengths >8 mm. All yolk-sac larvae collected from Montsweag Bay during March had a single vertical band of melanistic pigment across the postanal region and were <5.2 mm long.

Since *L. putnami* spawns from December through February while *P. americanus* spawns from March through May and eggs take 2 or 3 wk

to hatch (Bigelow and Schroeder 1953), larval flounders collected from Montsweag Bay in early March 1974 were tentatively identified as *L. putnami*. Yolk-sac larvae hatched from artificially spawned *L. putnami* eggs appeared identical to the field-collected larvae. Since the artificially spawned larvae were few and did not live beyond yolk absorption, larvae were collected from Montsweag Bay and reared in the laboratory to verify the identification. These larvae attained the adult dorsal and anal fin ray complement of *L. putnami* during the postflexion stage, verifying the identification. In April 1974, small yolk-sac flounder larvae matching descriptions of *P. americanus* (Martin and Drewry 1978) appeared in plankton samples collected from Montsweag Bay. Two of these larvae were reared in the laboratory to the postflexion stage and attained the adult dorsal and anal fin ray complements of *P. americanus*.

Counts that identify *L. putnami* and *P. americanus* (34-38 and 34-40 vertebrae, 48-60 and 60-76 dorsal fin rays, and 34-41 and 44-58 anal fin rays, respectively) were compiled from Jordan and Evermann (1898), Norman (1934), Bigelow and Schroeder (1953), Leim and Scott (1966), and this study.

LABORATORY OBSERVATIONS

Fertilized *L. putnami* eggs were nonadhesive and demersal in 23‰ water. Eggs ranged in diam-

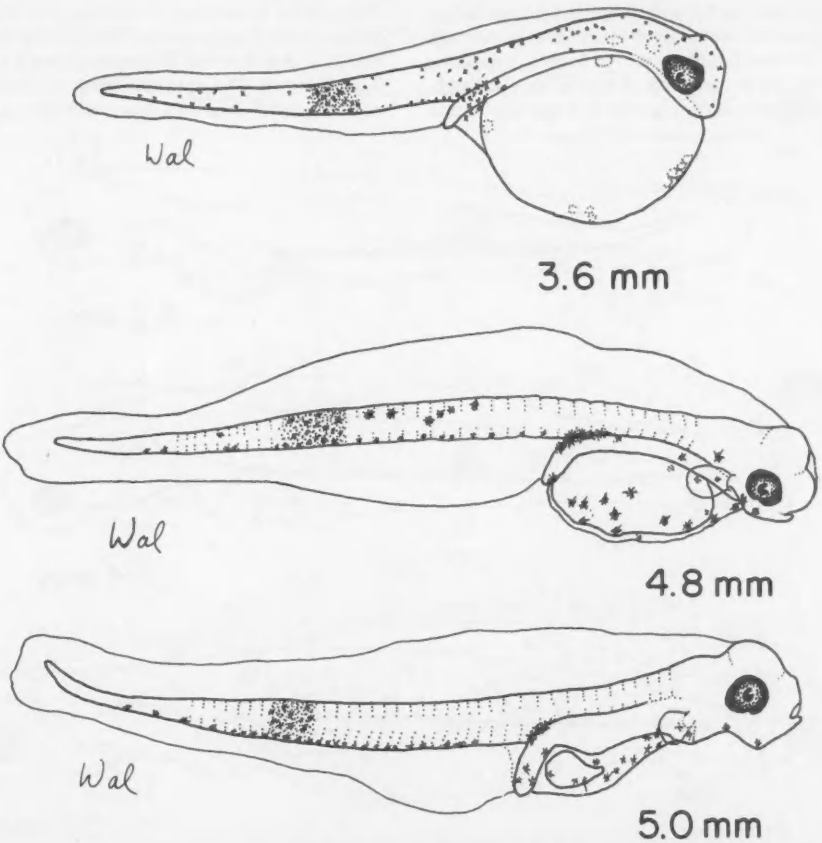

FIGURE 1.—Yolk-sac larvae of *Liopsetta putnami*.

eter from 1.1 to 1.4 mm, averaging 1.2 mm. Yolk diameter ranged from 0.9 to 1.2 mm, averaging 1.1 mm. No oil globules were obvious in newly fertilized eggs. At 5° C hatching began on the 25th day after fertilization. Newly hatched larvae were 3.1-3.6 mm long.

DISTINGUISHING FEATURES

Characters useful to distinguish larval *L. putnami* and *P. americanus* from other Gulf of Maine flatfishes are: number of myomeres, 34-38 and 38-40; hatching length, 3.1-3.6 mm and ≈2.4 mm; number of dorsal fin rays, 48-60 and 60-76; number of anal fin rays, 34-41 and 44-58; and presence of a single vertical band of melanistic pigment across the postanal region of both species.

Characters useful to distinguish yolk-sac larvae of *L. putnami* from *P. americanus* are: percentage snout to anus length/standard length, averaging 43.6% vs. 33.3%; presence of eye pigment at hatching vs. absence of eye pigment at hatching; length at hatching, 3.1-3.6 mm vs. ≈2.4 mm; and length at yolk-sac resorption, ≈5.2 mm vs. ≈3.7 mm.

Characters useful to distinguish larval *L. putnami* from *P. americanus* are: absence of internal melanophores over the notochord vs. presence of internal melanophores over the notochord; length at which gut loops, ≈5.5 mm vs. ≈4.3 mm; and absence vs. presence of anal fin pigmentation in specimens <6.3 mm.

GENERAL DEVELOPMENT
(Figures 1-8)

Reared *L. putnami* were 3.1-3.6 mm long at hatching. The smallest field-collected *L. putnami* larvae were ≈3.5 mm long. Newly hatched field-collected *P. americanus* larvae were ≈2.4 mm long. The yolk sac is resorbed by ≈5.2 and ≈3.7 mm in *L. putnami* and *P. americanus*. The gut loops by ≈5.5 mm in *L. putnami* and between 4.2 and 4.4 mm in *P. americanus*. The notochord begins to flex in *L. putnami* and *P. americanus* at ≈6.0 and ≈5.0 mm;

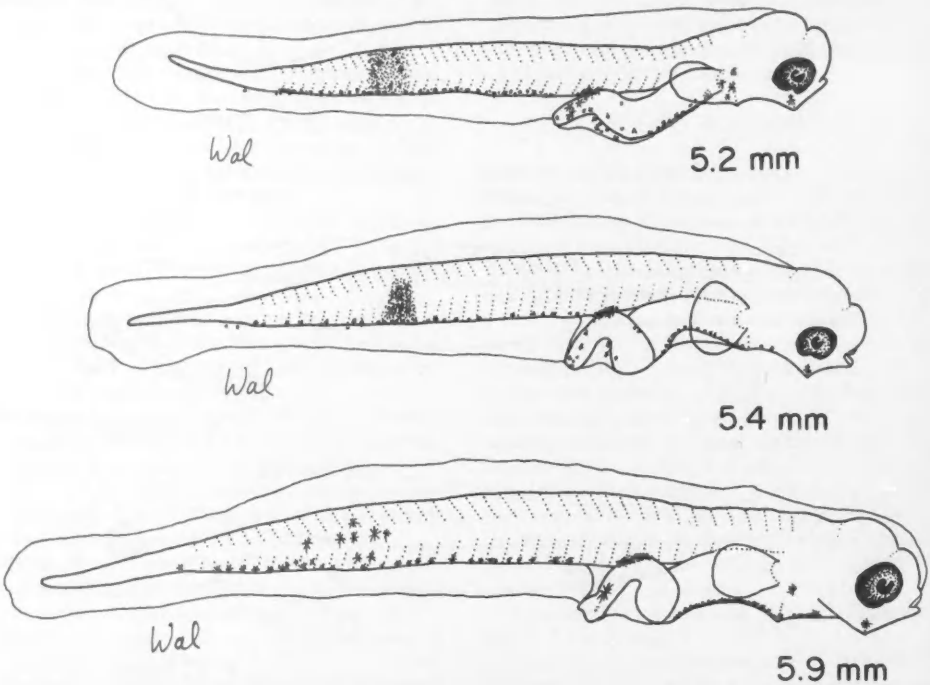

FIGURE 2.—Preflexion larvae of *Liopsetta putnami*.

flexion is completed by ≈7.1 and ≈6.6 mm; and the free tip of the notochord disappears by 7.6 and 7.3 mm. Transition from pelagic to benthic habit occurs at ≈7.3 mm in *L. putnami*. The largest pelagic field-collected *L. putnami* larva was 7.3 mm, and the largest specimen, 7.6 mm, had assumed the benthic habit in the laboratory. Transition from pelagic to benthic habit usually occurs between 6.0 and 7.0 mm in *P. americanus*. The smallest benthic-collected *P. americanus* was 5.7 mm, and the largest pelagic-collected larva was 7.4 mm long. Formation of pectoral and pelvic fin rays is completed between 8.5 and 13.0 mm (Laszlo 1972) in *L. putnami* and by ≈13 mm in *P. americanus*, marking the end of the transformation and beginning of the juvenile period.

MORPHOLOGY
(Tables 1-3)

Various body parts were measured on 40 *L. putnami* (3.1-7.6 mm) and 64 *P. americanus* (2.4-7.3 mm) larvae to examine developmental morphology. Body proportions are summarized and compared in Table 3.

The most important morphological character for separating *L. putnami* from *P. americanus*, particularly during the yolk-sac and preflexion

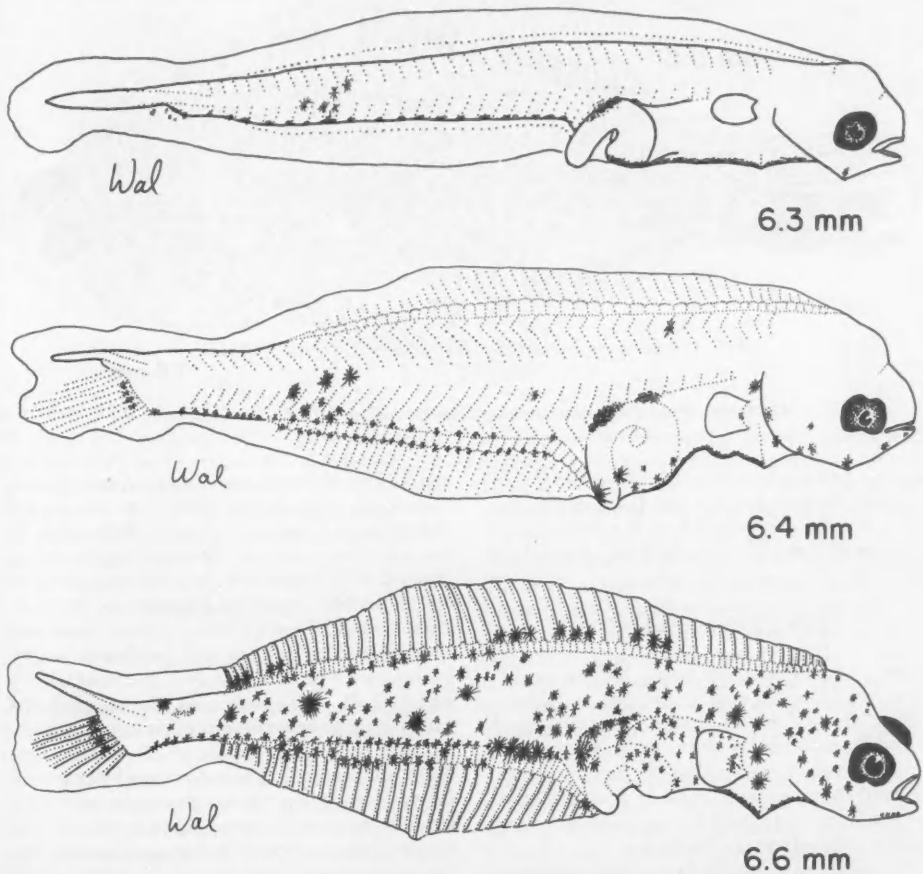

FIGURE 3.—Flexion larvae of *Liopsetta putnami*.

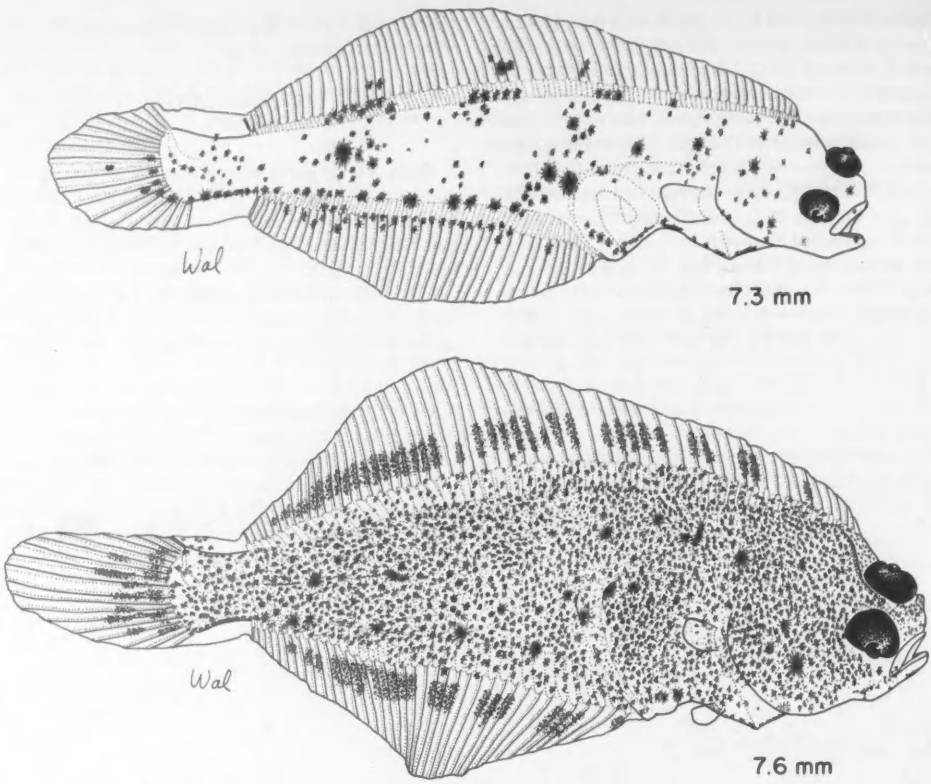

FIGURE 4.—Postflexion and transforming larvae (7.1 and 7.6 mm) of *Liopsetta putnami*.

stages, is snout to anus length/standard length. In *L. putnami* it averages 43.6 and 41.2% for yolk-sac and preflexion larvae while in *P. americanus* it averages 33.3 and 37.6% for yolk-sac and preflexion larvae.

FIN DEVELOPMENT

Newly hatched larvae of both *L. putnami* and *P. americanus* have an undifferentiated fin fold extending along the body midline from the head around the notochord tip to the anus. No other fins were observed on the smallest *L. putnami* larva (3.1 mm); however, the smallest *P. americanus* larva (2.4 mm) and a 3.8 mm *L. putnami* larva had undifferentiated pectoral fin folds.

Pectoral fin rays are the first to begin development in both *L. putnami* and *P. americanus*, by 5.2 and 5.3 mm. However, pectoral fin rays are the last to complete development, completed between 8.5 and 13 mm in *L. putnami* (Laszlo 1972) and by 13 mm in *P. americanus*. Pectoral fin length is greatest in both species during the preflexion and flexion periods, averaging 7.8 and 7.1% SL in *L. putnami* and 7.7 and 7.8% SL in *P. americanus*, and shortest during yolk-sac and postflexion stages, averaging 3.8 and 5.0% SL in *L. putnami* and 3.0 and 4.7% SL in *P. americanus*. Dorsal, anal, and caudal fin rays begin development in preflexion *L. putnami* and *P. americanus* at ≈5.9 and ≈5.6 mm. Adult complements of dorsal and anal fin rays and principal caudal fin rays are present by ≈8 and ≈7 mm. Fin rays within dorsal and anal fins of both species seem to form simultaneously except the two or three posteriormost rays in each fin which form last. Principal caudal fin rays form first and

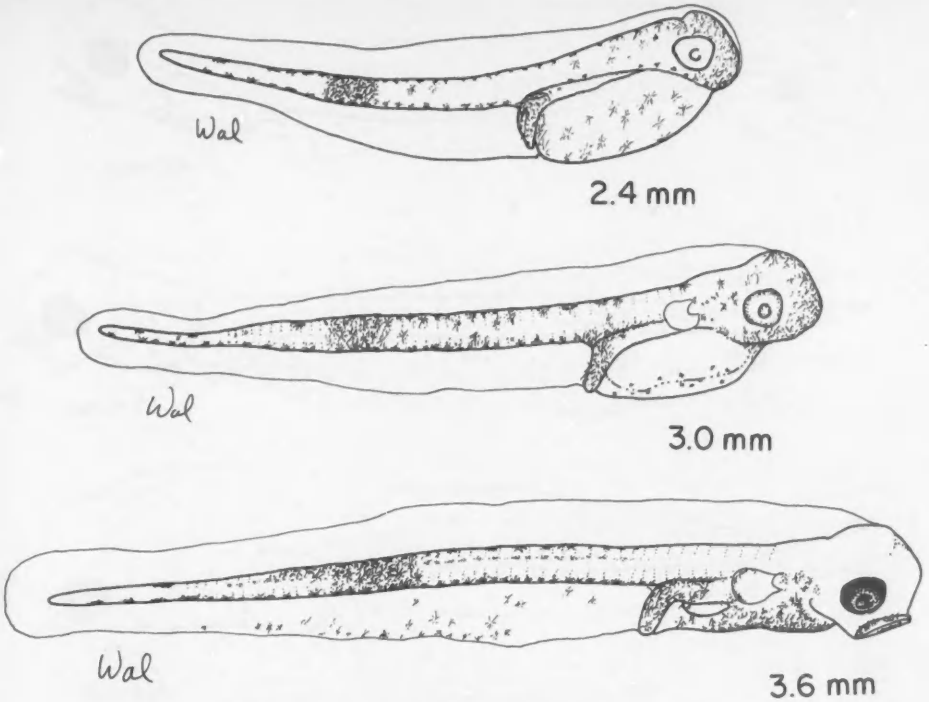

FIGURE 5.—Yolk-sac larvae of *Pseudopleuronectes americanus*.

secondary rays are gradually added anteriorly. The pelvic fin bud appears at ≈7 mm in postflexion *L. putnami* larvae. Fin rays begin to develop by 7.6 mm, and development is completed by 13 mm (Laszlo 1972). The pelvic fin bud appears at ≈6.6 mm in postflexion *P. americanus* larvae; and development is complete by 7.3 mm.

PIGMENTATION

Liopsetta putnami

The eyes of *L. putnami* are darkly pigmented at hatching. Small external melanophores are scattered over the head of the smallest larva (3.1 mm). These melanophores appear to migrate ventrolaterally, appearing on the ventral surface of the head between the isthmus and the cleithrum by ≈4.7 mm, and are aligned here on all specimens >5.4 mm long. This row often appears as a solid line of pigment due to the expanded condition of individual melanophores. A melanophore appears at the angle of the lower jaw between 4.8 and 5.4 mm, and one or two melanophores are present at this location on all specimens >5.4 mm. One or two melanophores are present at the tip of the lower jaw on most specimens >5.8 mm. A large stellate melanophore appears below the lateral midline of the head, anterior to the cleithrum at 5.2 mm. Larvae >5.4 mm often have 4-6 melanophores, internal and external, in this area. A few external melanophores appear scattered over the head, on and under the operculum, by 7.3 mm. Flexion and postflexion larvae >6.6 mm rapidly acquire the dense scattering of external melanophores characteristic of juveniles.

In the abdominal region small external melanophores scattered over the dorsolateral surfaces of the hindgut are present on the smallest larva (3.1 mm). An internal patch over the hindgut is present on all specimens in the series. The small external melanophores migrate ventrolaterally

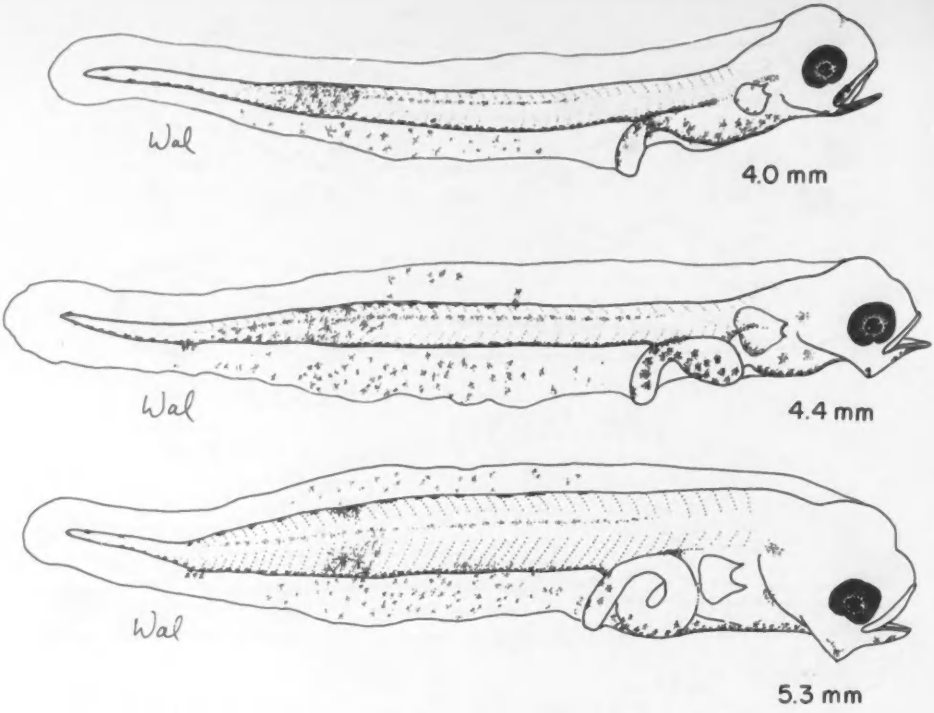

FIGURE 6.—Preflexion larvae (4.0 and 4.4 mm) and flexion larva (5.3 mm) of *Pseudopleuronectes americanus*.

becoming scattered on only the ventral surface of the body and yolk sac by 4.8 mm and form a row along the ventral midline on all specimens larger than ≈5.2 mm. This row extends from the cleithrum, where it is continuous with the row on the ventral midline of the head, to the center of the abdominal region where it becomes indistinct, merging with a group of melanophores scattered on the ventrolateral body surface between 6.6 and 7.0 mm. Specimens >7.0 mm rapidly acquire the dense scattering of external melanophores over the body surface characteristic of juveniles.

Small external melanophores are scattered over the postanal region, and a vertical band of concentrated melanophores of various sizes is present across the center of the postanal region in the smallest larva (3.1 mm). The scattered external melanophores migrate ventrolaterally and are present only on the ventrolateral surfaces by ≈4.6 mm. An irregular row of melanophores extends from the anus to the vertical pigment band along both sides of the ventral midline, and a single irregular row of melanophores along the ventral midline extends posteriorly from the pigment band on specimens 4.3-5.4 mm long. Usually one to several small melanophores appear somewhat separated from the row and located just anterior to the notochord tip. The vertical pigment band is distinct on larvae <5.4 mm, but it is usually represented by only a few large stellate melanophores on larger larvae. These melanophores become indistinguishable from other external melanophores which become scattered over the body on large larvae, >6.6 mm, indicating the initial development of the juvenile pigment pattern.

The fin folds of the smallest *L. putnami* larva are not pigmented. At ≈5.2 mm one or two melanophores move from the body onto the fin membrane just anteroventral to the notochord tip.

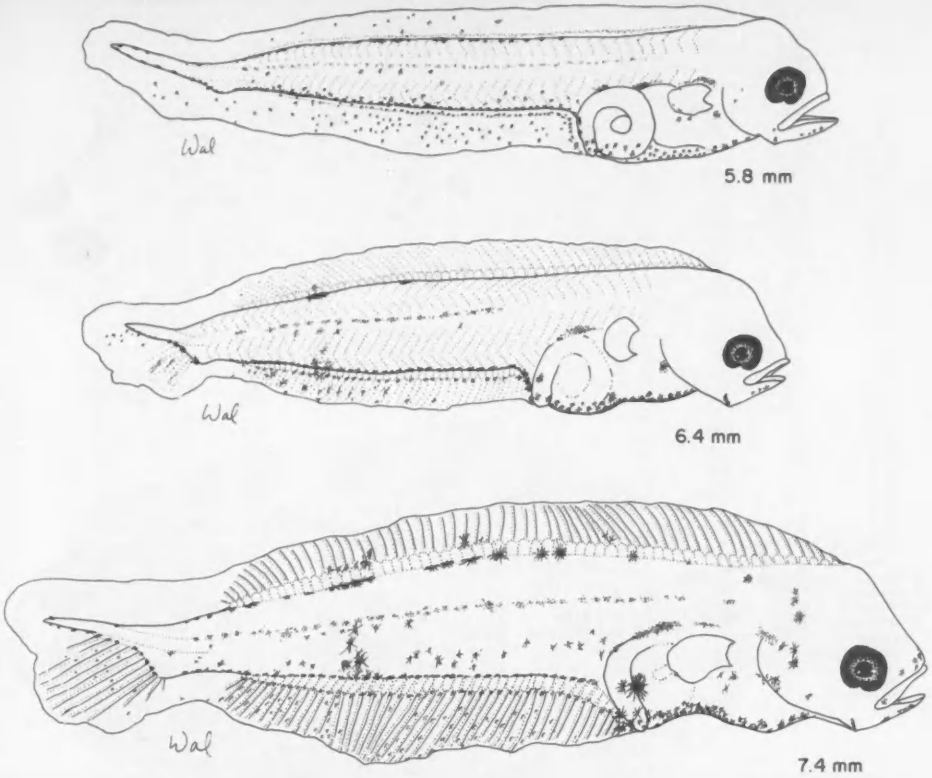

FIGURE 7.—Flexion larvae of *Pseudopleuronectes americanus*.

Several additional melanophores appear at this location by 6.3 mm and appear on the caudal fin near the base of the caudal fin rays after they form. As the pterygiophores associated with the anal fin rays begin to develop, between 6.3 and 6.4 mm, melanophores separate from the postanal ventral midline rows and appear as an irregular row along the distal margins of the pterygiophores and along the bases of the dorsal and anal rays by 6.6 mm. A broken band of melanophores develops in the proximal one-third of the dorsal and anal fins by 7.6 mm.

Scattered metallic yellow chromatophores were present over the head and body of newly hatched larvae. These chromatophores disappear soon after preservation in Formalin. No additional observations of chromatophore patterns were possible on larger field-collected larvae.

Pseudopleuronectes americanus

The eyes of *P. americanus* lack pigmentation at hatching (≈2.4 mm). Pigmentation begins to appear in the eyes of *P. americanus* at ≈2.9 mm, and the eyes are completely pigmented by 3.5 mm. Expanded external melanophores are scattered over the head of the smallest larva (2.4 mm). These melanophores are faint and may be difficult to see. Melanophores over the dorsolateral surfaces of the head disappear by ≈3.5 mm. A few melanophores remain on the upper and lower jaws and along the ventral midline of the head (gular and isthmus regions). No evidence of melanophore migration was observed in *P. americanus*. One to several internal melanophores are present along the anterior edge of the cleithrum often appearing under the operculum on larvae >2.6 mm. One or two

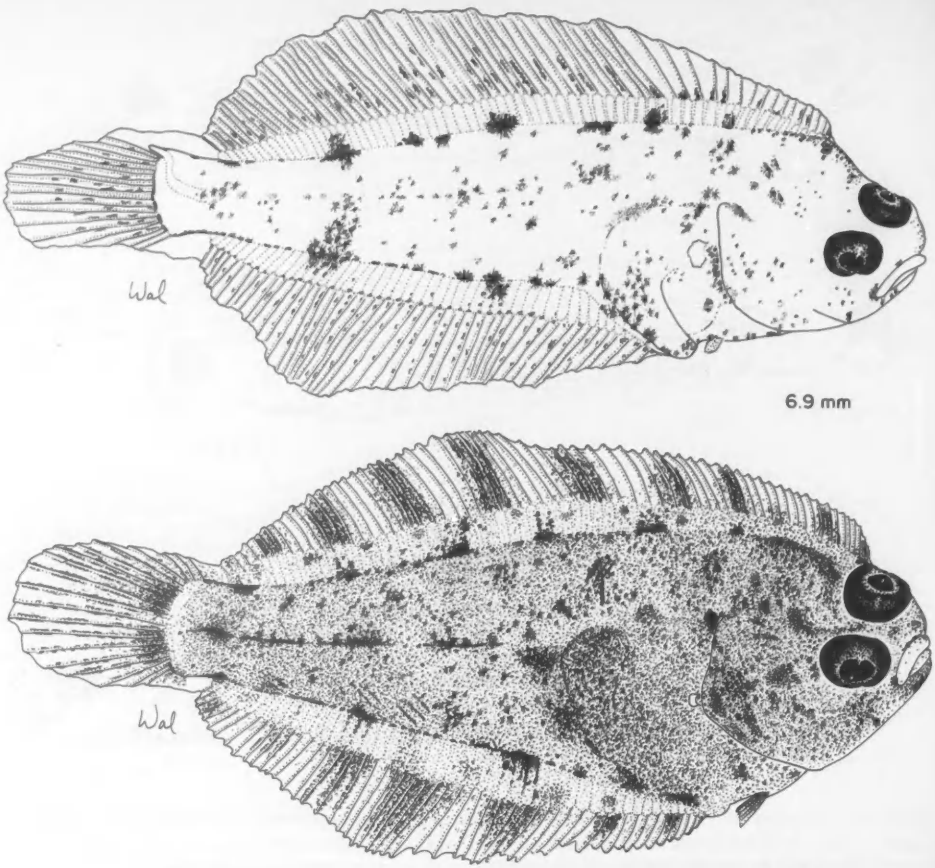

FIGURE 8.—Flexion, transforming, larva (6.9 mm) and postflexion, transforming, larva (9.8 mm) of *Pseudopleuronectes americanus*.

melanophores are present at the articulation of the lower jaw on larvae >3.4 mm. A few external melanophores appear on the snout and operculum of preflexion larvae >6.6 mm. Postflexion larvae (>5.8 mm) rapidly acquire a covering of external melanophores, characteristic of juveniles, as transformation proceeds.

External melanophores are scattered over the abdominal region of the smallest larva (2.4 mm) with greatest concentrations along the dorsal surface of the body and on the ventrolateral surface of the yolk sac. Internal melanophores are present in a patch over the posterior hindgut near the anus and over the middle of the gut. By 3.6 mm pigmentation disappears from the dorsolateral surface of the abdominal region, and the melanophores which had been scattered over the yolk sac are on the ventrolateral surfaces of the body. Some of these form a row which is often expanded and appears as a solid line between the anus and the cleithrum with some on the ventrolateral surface on each side of the line. Also, by 3.6 mm, one to several internal melanophores appear in the vicinity of the pectoral fin base posterior to the cleithrum. By 4.4 mm, internal melanophores are present over the notochord in this region. No further pigmentation changes occur until external melanophores begin to appear scattered over

TABLE 1.—Measurements (millimeters) of larval *Liopsetta putnami*. Specimens above dashed line are yolk-sac larvae.

Standard length	Total length	Body depth at pectoral fin base	Body depth at anus	Maximum body depth at pectoral fin base	Maximum body depth at anus	Snout to anus length	Head length	Eye diameter	Upper jaw length	Snout length	Pectoral fin length
3.1	3.2	0.40	0.36	—	—	1.5	0.44	0.18	—	—	—
3.6	3.8	0.40	0.36	—	—	1.8	0.50	0.24	—	0.16	0.18
4.0	4.1	0.34	0.22	—	—	1.6	0.52	0.24	—	0.14	0.14
4.3	4.4	0.36	0.24	—	—	2.0	0.56	0.24	—	0.16	—
4.4	4.5	0.38	0.26	—	—	1.8	0.60	0.26	—	0.22	0.10
4.6	4.8	0.40	0.24	—	—	1.8	0.60	0.24	—	0.16	0.18
4.8	5.0	0.50	0.28	—	—	1.9	0.62	0.26	0.14	0.14	0.34
4.8	5.0	0.54	0.28	—	—	—	0.64	0.26	—	0.12	0.14
4.8	5.0	0.46	0.26	—	—	2.1	0.62	0.24	0.14	0.18	0.16
4.9	5.2	0.40	0.26	—	—	2.2	0.64	0.26	—	0.16	0.18
4.9	5.1	0.40	0.26	—	—	2.1	0.60	0.26	—	0.16	0.12
5.0	5.1	0.38	0.30	—	—	2.2	0.68	0.26	—	0.20	0.18
[1]5.2	5.3	0.46	0.32	—	—	2.2	0.74	0.26	0.20	0.18	0.30
[1]5.2	5.3	0.54	0.34	—	—	2.4	0.80	0.28	0.18	0.16	0.32
[1]5.4	5.7	0.62	0.40	—	—	2.4	0.80	0.29	0.16	0.12	0.38
[1]5.4	5.7	0.66	0.42	—	—	2.1	0.80	0.26	0.20	0.14	0.36
[1]5.5	5.8	0.82	0.62	—	—	2.1	0.96	0.30	0.18	0.10	0.52
[1]5.5	5.7	0.76	0.60	—	—	2.4	1.0	0.29	0.30	0.16	0.56
[1]5.7	5.9	0.74	0.60	—	—	2.4	1.1	0.28	0.26	0.12	0.52
[1]5.8	6.0	0.78	0.62	—	—	2.3	1.0	0.30	0.38	0.20	0.52
[1]5.9	6.2	0.74	0.44	—	—	2.4	0.96	0.27	0.28	0.16	0.44
[2]5.9	6.2	0.80	0.70	—	—	2.6	1.2	0.30	0.32	0.20	0.40
[1]5.9	6.2	0.78	0.56	—	—	2.3	1.1	0.30	0.36	0.18	0.40
[2]6.2	6.3	0.98	0.90	1.0	0.94	2.5	1.1	0.32	0.42	0.26	0.54
[1]6.3	6.6	0.78	0.56	—	—	2.5	1.0	0.30	0.32	0.16	0.48
[1]6.4	6.6	1.0	0.92	1.1	0.94	2.7	1.2	0.32	0.46	0.24	0.50
[1]6.5	6.7	0.74	0.52	—	—	2.7	1.1	0.32	0.30	0.16	0.46
[1]6.6	6.8	0.78	0.60	—	—	2.5	1.0	0.31	0.30	0.14	0.54
[2]6.6	6.9	1.0	0.80	1.1	0.86	2.7	1.2	0.33	0.40	0.20	0.46
[2]6.6	6.8	1.1	1.1	1.2	1.1	2.8	1.4	0.34	0.42	0.22	0.54
[2]6.7	6.9	0.92	0.80	0.96	0.86	2.7	1.0	0.32	0.40	0.20	0.44
[2]6.8	7.1	0.84	0.72	0.89	0.74	2.8	1.2	0.32	0.32	0.18	0.40
[2]6.9	7.1	0.92	0.76	0.96	0.80	2.6	1.2	0.34	0.40	0.20	0.50
[2]7.0	7.4	1.1	1.1	1.2	1.1	2.8	1.3	0.34	0.40	0.16	0.52
[2]7.0	7.3	1.2	1.1	1.2	1.2	2.8	1.4	0.32	0.40	0.20	0.50
[2]7.0	7.4	1.1	1.0	1.1	1.1	2.8	1.3	0.32	0.40	0.18	0.50
[2]7.1	8.1	1.5	1.4	1.6	1.5	2.6	1.5	0.36	0.44	0.26	0.60
[2]7.3	7.6	1.1	1.0	1.2	1.1	3.0	1.3	0.36	0.40	0.18	0.50
[2]7.3	7.5	1.1	1.0	1.2	1.1	2.8	1.3	0.34	0.40	0.20	0.48
[2]7.6	9.3	—	—	2.4	2.4	2.7	2.1	0.54	0.56	0.28	0.24

[1] = preflexion larvae; [2] = flexion larvae; [3] = postflexion larvae.

the abdominal region of preflexion larvae, >6.2 mm, as metamorphosis begins and the juvenile pattern of dense melanophore covering begins to develop.

A vertical band of concentrated melanophores of various sizes is present across the center of the postanal region in the smallest larva (2.4 mm). External melanophores are aligned in irregular rows on both sides of the ventral midline between the anus and the postanal band. A single irregular row of melanophores extends along the ventral surface from the vertical band nearly to the notochord tip. An irregular row is also present along the dorsal midline extending posteriorly nearly to the notochord tip. Only a few scattered melanophores appear laterally. A row of internal melanophores over the notochord is present on all larvae longer than ≈3.2 mm. The postanal band becomes less distinct, usually represented by only a few large stellate melanophores, in larvae >5.0 mm. Scattered external melanophores begin to appear over the lateral surfaces of preflexion larvae >5.6 mm and continue to increase in number through the larval period. Concentrated pigment spots develop along the dorsal and ventral body surfaces in transforming larvae >5.8 mm.

The fin folds of the smallest *P. americanus* larva are not pigmented. Various authors (Sullivan 1915; Breder 1924; Bigelow and Schroeder 1953; Lippson and Moran 1974) have illustrated small larvae with melanophores extending onto the dorsal and anal fin folds (probably no melanophores were centered on the fin folds) from the vertical postanal band. Their illustrations were of artificially reared larvae. I observed no melanophores extending onto the dorsal and anal fin folds of field-collected larvae; however, reared larvae commonly have somewhat increased pigment due mostly to light conditions which can be altered to change the size of melanophores (Milos and Dingle 1978). A few small melanophores appear along the margin of the pectoral fin fold at 3.5 mm and disappear

TALBE 2.—Measurements (millimeters) of larval *Pseudopleuronectes americanus*. Specimens above dashed line are yolk-sac larvae.

Standard length	Total length	Body depth at pectoral fin base	Body depth at anus	Maximum body depth at pectoral fin base	Maximum body depth at anus	Snout to anus length	Head length	Eye diameter	Upper jaw length	Snout length	Pectoral fin length
2.4	2.5	0.20	0.14	—	—	0.92	0.39	0.17	—	0.08	0.05
2.6	2.7	0.18	0.15	—	—	0.92	0.38	0.16	—	0.10	0.04
2.6	2.6	0.24	0.14	—	—	0.85	0.39	0.17	—	0.11	0.04
2.7	2.7	0.24	0.15	—	—	0.94	0.42	0.17	—	0.10	0.04
2.8	2.8	0.25	0.14	—	—	0.90	0.39	0.17	—	0.10	0.08
2.8	2.9	0.24	0.14	—	—	0.98	0.39	0.16	—	0.10	0.05
2.8	3.0	0.24	0.15	—	—	1.0	0.42	0.18	0.16	0.12	—
2.9	3.0	0.19	0.13	—	—	0.96	0.39	0.17	0.14	0.12	0.06
2.9	3.0	0.21	0.14	—	—	0.90	0.40	0.18	—	0.12	0.04
2.9	3.0	0.24	0.15	—	—	0.96	0.42	0.18	0.16	0.14	0.06
3.0	3.2	0.24	0.15	—	—	1.0	0.42	0.18	0.18	0.14	0.05
3.3	3.4	0.25	0.14	—	—	1.0	0.42	0.18	0.18	0.10	0.06
3.3	3.5	0.34	0.15	—	—	1.0	0.42	0.18	0.18	0.08	0.10
3.4	3.6	0.36	0.14	—	—	1.1	0.42	0.20	0.18	0.08	0.10
3.4	3.6	0.38	0.15	—	—	1.2	0.46	0.20	0.19	0.10	0.20
3.5	3.7	0.33	0.14	—	—	1.1	0.44	0.18	0.17	0.09	0.20
3.5	3.7	0.34	0.15	—	—	1.2	0.46	0.20	0.20	0.09	0.20
3.5	3.7	0.34	0.15	—	—	1.1	0.45	0.18	0.19	0.10	0.19
3.6	3.8	0.33	0.14	—	—	1.2	0.47	0.20	0.21	0.13	0.20
[1]3.7	3.9	0.48	0.24	—	—	1.4	0.66	0.24	0.26	0.12	0.30
[1]4.0	4.3	0.42	0.19	—	—	1.5	0.62	—	0.26	—	0.26
[1]4.2	4.3	0.60	0.30	—	—	1.5	0.76	0.27	0.26	0.18	0.32
[1]4.4	4.5	0.50	0.22	—	—	1.6	0.70	0.26	0.22	0.14	0.32
[1]4.4	4.5	0.50	0.22	—	—	1.5	0.68	0.24	0.22	0.15	0.30
[1]4.5	4.6	0.66	0.32	—	—	1.6	0.80	0.28	0.24	0.12	—
[1]4.5	4.6	0.70	0.35	—	—	1.7	0.82	0.27	0.26	0.18	0.30
[1]4.6	4.7	0.74	0.38	—	—	1.8	0.92	0.32	0.38	0.20	0.28
[2]4.8	4.9	0.80	0.46	—	—	1.8	0.86	0.31	0.30	0.18	0.30
[1]4.9	5.2	0.78	0.44	—	—	1.8	0.98	—	—	—	0.40
[1]4.9	5.2	—	—	—	—	2.0	1.1	0.34	0.32	0.20	0.45
[1]5.1	5.3	0.85	0.54	—	—	2.0	1.0	0.33	0.32	0.14	0.44
[1]5.2	5.4	0.96	0.64	—	—	2.0	1.0	0.34	0.36	0.24	0.44
[2]5.3	5.5	0.94	0.56	—	—	2.1	0.98	0.33	0.34	0.22	0.44
[1]5.4	5.5	0.90	0.60	—	—	2.1	1.1	0.33	0.35	0.18	—
[2]5.6	5.7	1.1	0.82	—	—	2.3	1.2	0.34	0.40	0.24	0.48
[1]5.7	5.8	1.1	0.78	—	—	2.1	1.2	0.34	0.40	0.22	0.45
[1]5.7	5.8	1.1	0.72	—	—	2.2	1.1	0.34	0.40	0.26	0.46
[2]5.8	6.1	1.1	0.70	—	—	2.3	1.2	0.36	0.36	0.20	0.52
[2]6.0	6.2	1.1	0.80	—	—	2.3	1.3	0.36	0.36	0.20	0.48
[2]6.2	6.3	1.3	0.88	—	1.0	2.4	1.3	0.36	0.42	0.26	0.55
[2]6.3	6.4	1.3	0.98	1.4	1.2	2.4	1.4	0.40	0.48	0.26	0.54
[2]6.3	6.4	1.3	0.88	—	1.1	2.4	1.4	0.36	0.44	0.28	0.50
[2]6.4	6.5	1.2	0.86	1.3	1.1	2.4	1.3	0.34	0.40	0.20	0.48
[2]6.5	6.7	1.2	0.84	1.3	1.0	2.6	1.4	0.38	0.42	0.26	0.42
[2]6.6	6.7	1.3	0.96	1.4	1.2	2.5	1.4	0.38	0.42	0.22	0.52
[2]6.6	6.8	1.4	1.1	1.6	1.5	2.4	1.6	0.39	0.48	0.28	0.58
[2]6.8	6.9	1.3	1.0	1.4	1.3	2.5	1.5	0.38	0.40	0.26	0.50
[2]6.9	7.2	1.3	0.96	1.4	1.2	2.6	1.5	0.40	0.46	0.27	0.52
[2]7.0	7.3	1.4	1.1	1.5	1.2	2.7	1.5	0.41	0.44	0.28	0.64
[2]7.1	7.3	1.3	0.94	1.4	1.2	2.6	1.3	0.39	0.44	0.24	0.56
[2]7.3	7.8	1.7	1.4	1.8	1.7	2.6	1.8	0.46	0.44	0.32	0.54
[2]7.4	7.7	1.4	1.1	1.5	1.2	2.4	1.5	0.38	0.44	0.26	0.50
[3]5.7	—	1.7	1.2	1.8	1.6	2.0	1.6	0.48	0.49	0.22	—
[3]6.0	—	1.7	1.3	1.7	1.7	2.4	1.7	0.46	0.48	0.34	0.40
[3]6.2	—	1.9	1.3	2.2	1.8	2.3	1.7	0.46	0.46	0.38	0.34
[3]6.4	—	2.2	1.5	2.4	2.1	2.3	1.7	0.54	0.51	0.34	0.10
[3]6.6	7.7	1.6	1.3	1.8	1.7	2.4	1.8	0.46	0.44	0.38	0.42
[3]6.6	—	1.7	1.4	1.8	1.9	2.5	1.8	0.48	0.44	0.34	0.41
[3]6.9	8.2	1.9	1.5	2.1	2.1	2.3	1.8	0.50	0.46	0.40	0.30
[3]7.0	8.4	1.9	1.5	2.0	2.1	2.4	1.8	0.46	0.42	0.36	0.30
[3]7.0	8.4	2.2	1.7	2.4	2.4	2.2	2.0	0.58	0.56	0.44	0.10
[3]7.1	8.5	2.0	1.5	2.1	1.8	2.4	1.9	0.51	0.40	0.40	0.20
[3]7.3	7.9	2.5	1.8	2.6	2.2	2.4	2.0	0.62	0.38	0.38	—

[1] = preflexion larvae; [2] = flexion larvae; [3] = postflexion larvae.

again in flexion larvae by ≈6.4 mm. Scattered melanophores appear on the anal fin fold at 3.6 mm, and a few appear at the center of the dorsal fin fold at ≈4.2 mm. These melanophores remain through the larval period with pigment bars, characteristic of juveniles, developing on the dorsal and anal fins in flexion and postflexion larvae >7.3 mm. By 4.4 mm a few melanophores appear on the fin fold at about the notochord flexion point. These melanophores increase in number with development and are visible on the caudal fin during and after development of the caudal fin rays.

TABLE 3.—Body proportions of larval *Liopsetta putnami* and *Pseudopleuronectes americanus*. Values given are percentage of standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from Tables 1 and 2.

Item	*Liopsetta putnami*	*Pseudopleuronectes americanus*
Body depth at pectoral fin base/SL:		
Yolk sac	9.4± 1.61(7.6-12.9)	8.8±1.23(6.6-11.2)
Preflexion	12.5± 1.74(8.8-13.8)	15.2±2.87(10.5-19.3)
Flexion	15.4± 2.14(12.4-20.5)	19.3±1.49(16.7-23.3)
Postflexion	23.6±11.38(15.5-31.6)	28.6±3.85(21.2-34.2)
Body depth at anus/SL:		
Yolk sac	6.4± 2.08(5.2-11.6)	4.8±0.61(3.9-5.9)
Preflexion	9.2± 2.22(6.2-14.4)	8.6±2.99(4.8-13.7)
Flexion	13.5± 1.99(11.0-16.7)	13.9±2.11(9.6-19.2)
Postflexion	25.6± 8.41(19.7-31.6)	21.3±1.83(16.7-24.3)
Maximum body depth at pectoral fin base/SL:		
Yolk sac	9.4± 1.61(7.6-12.9)	8.8±1.23(6.6-11.2)
Preflexion	12.6± 1.89(8.8-16.6)	15.2±2.87(10.5-19.3)
Flexion	15.6± 1.52(13.1-17.6)	20.2±1.80(16.7-24.7)
Postflexion	28.1± 7.50(22.8-33.4)	31.1±4.45(24.2-38.4)
Maximum body depth at anus/SL:		
Yolk sac	6.4± 2.08(5.2-11.6)	4.8±6.09(3.9-5.9)
Preflexion	9.2± 2.28(6.2-14.7)	8.6±2.99(4.8-13.7)
Flexion	14.1± 2.00(10.9-17.0)	16.1±3.35(10.6-23.3)
Postflexion	26.8± 7.67(21.4-32.1)	28.8±3.17(22.7-34.3)
Snout to anus length/SL:		
Yolk sac	43.6± 3.62(39.1-50.0)	33.3±2.03(30.3-37.7)
Preflexion	41.2± 2.46(37.9-46.2)	37.6±1.72(34.1-40.8)
Flexion	40.5± 1.67(36.6-44.1)	37.9±1.95(32.4-41.1)
Postflexion	36.0± 0.78(35.5-36.6)	35.4±2.39(24.2-28.6)
Head length/SL:		
Yolk sac	13.2± 0.53(12.2-14.2)	13.9±1.05(12.4-16.0)
Preflexion	15.4± 4.31(14.2-16.8)	18.7±2.03(15.5-22.4)
Flexion	18.3± 1.63(14.9-21.2)	21.0±1.61(18.3-24.7)
Postflexion	24.4± 4.60(21.1-27.6)	27.0±1.22(24.2-28.6)
Eye diameter/HL:		
Yolk sac	41.9± 2.87(38.2-48.0)	43.1±1.81(40.0-47.6)
Preflexion	31.2± 3.57(25.5-37.5)	33.4±2.55(31.1-37.1)
Flexion	26.8± 2.28(24.3-32.0)	28.3±2.71(25.0-33.7)
Postflexion	24.8± 1.20(24.0-25.7)	27.1±2.36(24.0-31.4)
Upper jaw length/HL:		
Yolk sac	22.6± 0.00(22.6)	41.0±2.80(35.9-44.7)
Preflexion	28.2± 5.96(18.8-38.3)	34.5±4.18(30.0-41.9)
Flexion	31.5± 3.57(26.7-40.0)	31.3±2.47(26.7-34.7)
Postflexion	28.0± 1.84(26.7-29.3)	26.0±3.67(19.0-30.6)
Snout length/HL:		
Yolk sac	27.5± 4.69(18.8-36.7)	25.2±4.71(19.0-33.3)
Preflexion	16.8± 3.72(10.4-24.3)	19.8±3.37(14.0-24.0)
Flexion	16.2± 3.05(12.3-20.0)	18.3±1.92(15.4-22.4)
Postflexion	15.3± 2.83(13.3-17.3)	19.8±2.40(13.8-22.4)
Pectoral fin length/SL:		
Yolk sac	3.8± 1.38(2.4-7.1)	3.0±1.75(1.4-5.9)
Preflexion	7.8± 1.30(5.8-10.2)	7.7±0.92(6.1-9.2)
Flexion	7.1± 0.74(5.9-8.5)	7.8±0.85(6.2-9.1)
Postflexion	5.0± 2.55(3.2-6.8)	4.7±2.48(0.8-8.8)

Melanophore numbers on the caudal fin membrane increase through flexion and postflexion periods with the entire fin becoming covered with melanophores, including an intense pigment patch near the fin base, by 9.8 mm.

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SEASONALITY OF FISHES OCCUPYING A SURF ZONE HABITAT IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

The ichthyofauna occupying the surf zone habitat of Horn Island, Mississippi, between 1975 and 1977 was dominated by immature clupeiform fishes. The dusky anchovy, *Anchoa lyolepis*, and the scaled sardine, *Harengula jaguana*, together constituted 80.2% of the 154,469 fishes collected. The greatest number of fishes were collected in the late spring and summer, followed by a secondary peak in late winter. Occurrence of the fishes within the surf zone is divided into three categories according to seasonal utilization: spring and summer, summer only, and winter. Factors affecting numerical abundance within the surf zone differed among the most frequently appearing species. Differences in the numbers of clupeiform fishes—*A. lyolepis*; *A. hepsetus*, striped anchovy; and *H. jaguana*—were more closely associated with diel changes including tidal stage and time of day. The abundance of the Florida pompano, *Trachinotus carolinus*, and the gulf kingfish, *Menticirrhus littoralis*, were more dependent upon seasonal effects such as temperature.

Relatively few studies have investigated the role of exposed surf zone habitats in the early life history of fishes. While Springer and Woodburn (1960) described the surf zone region as an "extreme habitat offering little environmental diversity," this habitat does provide several benefits to fishes. Advantages suggested by Warfel and Merriman (1944) included the abundance of food (concentrated by incoming tides), increased metabolic efficiency via heat acquisition, and protection from predation.

Surf zone ichthyofaunas are numerically dominated by relatively few species. For instance, McFarland (1963) stated that 60-80% of the ichthyofauna occupying the surf regions along the south Atlantic and Texas coasts was comprised of only a few species. Gunter (1958) found high similarity in species composition between Mustang Island, Texas, and Atlantic coast surf zones and suggested that the surf zone region was dominated by a small group of species which remained relatively constant over wide geographical areas.

Much of the literature regarding shore zone fishes is restricted to either descriptions of species occurrence or seasonal characterizations, seldom exceeding one annual cycle. Reid (1955a, b), Schaefer (1967), and Hillman et al. (1977) have sampled the same habitats in successive seasons and have observed annual changes in species composition. Fewer studies have attempted to relate physical or biological parameters to the abundance of fishes within the shallow beach habitat. Gunter (1945) and Warfel and Merriman (1944) attributed the distinct seasonal fluctuations in fish abundance to temperature. Both Anderson et al. (1977) and de Sylva,[3] using multiple regression analyses and crosstabulation, respectively, also indicated that temperature was a significant factor in determining seasonal abundance of the most numerous fish species.

The present study describes seasonal and annual variations in fish species composition and the factors affecting fish occurrences within the surf zone of Horn Island, Miss., a barrier island in the northern Gulf of Mexico.

METHODS

The study area was located along the southern shore of Horn Island, Jackson County, Miss. Horn Island is in a chain of barrier islands lying parallel to the Mississippi-Alabama Gulf coast (Figure 1). The island lies approximately 14 km off the mainland and has a length of 19 km with a maximum width of 1.2 km. The beach is partially protected from oceanic wind-driven waves by a series of sand

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FIGURE 1.—Map of Horn Island, Jackson County, Miss., showing the four sampling areas. The southern side of the island represented the windward shore.

bars which extend the length of the island. The surf zone habitat is characterized by a sand substrate, the absence of any rooted vegetation, and sufficient wave activity to be categorized as a high energy beach (Odum and Copeland 1974).

We began sampling in April 1975 along the southwestern edge of the island (Station 1), and collections were made at about 7-wk intervals until November 1975. From May 1976 to November 1977 we sampled four stations along the windward shore of Horn Island (Figure 1) at about 5-wk intervals (Table 1). We also sampled sheltered beach areas adjacent to Stations 3 and 4 during the summer of 1976. All of the above collections were taken between 0900 and 1600 h c.s.t. (central standard time).

TABLE 1.—Sampling dates for fish taken from the surf zone habitat on the southern shore of Horn Island, Miss., between April 1975 and November 1977. Each collection represents a set of seine hauls at a specific location.

	1975		1976		1977	
Season	Date	No. of collections	Date	No. of collections	Date	No. of collections
Winter			13 Mar.	6	22 Jan.	4
					17 Mar.	5
Spring	12 Apr.	3	23 Apr.	4	28 Apr.	5
	21 June	2	28 May	7	27 May	8
Summer	12 Aug.	3	25 June	11	27 June	5
			23 July	8	23 July	5
			24 Aug.	5	17 Sept.	4
			2 Sept.	8		
Fall	18 Oct.	4	1 Oct.	6	23 Nov.	4
			4 Dec.	5		

Every month between March and September 1976 (excluding August) we sampled either Station 1, 3, or 4 over a 24-h period, taking samples at about 4-h intervals. The choice of station was based in part on the availability of a safe anchorage for our boat. In order to compare data throughout the study, collections made between 1600 and 0900 h were not included in seasonal or annual comparisons.

Fishes were collected with a 3.2 mm Ace[4] mesh bag seine measuring 9.1 × 1.8 m. Hauls were made perpendicular to the beach face beginning 16-18 m offshore. The area sampled extended from the swash zone to the midlongshore trough, and we made an effort to take regular samples only in areas directly exposed to surf. We continued seining at each location until no additional new species were collected; usually 5-9 hauls sufficed. Each collection at each location was thus comprised of a successive number of seine hauls. Fishes collected from all seine hauls at a single station were pooled for analysis. Catch-per-effort data from all stations were pooled to provide monthly means. The study included 613 seine hauls.

Species similarity by months was analyzed by the unpaired group arithmetic average clustering (UPGMA) method (Sneath and Sokal 1973). Only the 15 most abundant species, which were collected in at least 15% of the locations sampled, were analyzed. Pair similarity based on species presence or absence (Odum 1971) was determined by:

$$S = 2C/A + B$$

where C = number of species common to samples a and b,
A = number of species in sample a,
B = number of species in sample b.

We used stepwise multiple regression to define the dominant factors associated with the abundance (fish per seine haul) of the five most frequently occurring species. Environmental parameters selected as independent variables were

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

temperature, salinity, tide level, wave height, beach slope, wind speed, and wind direction. The latter two parameters represented means of the 4-wk period preceding each collection. Wind direction and velocity data were recorded at Keesler Air Force Base on the adjacent mainland. Tide level data were entered as the difference from mean low water and were from tide tables. Because of the absence of data regarding several environmental parameters, collections made during 1975 were not included in the regression analysis.

RESULTS

Annual and Seasonal Occurrence

During the 32-mo study period, 154,469 fishes, representing 14 orders, 42 families, and 76 species, were collected (Table 2). These were primarily late larvae and early juveniles, and only 1.1% exceeded 50 mm SL. The major families represented in the surf zone, in both percent occurrence and numbers collected, were the Engraulidae, Clupeidae,

TABLE 2.—Total number of fishes collected from the surf zone of Horn Island, Miss., between April 1975 and November 1977, and percentage frequency of species occurrence in the collections.

Species	1975	1976	1977	Total	Frequency of occurrence
Carcharhinidae					
Carcharhinus limbatus, blacktip shark		1		1	0.9
Dasyatidae					
Dasyatis sayi, bluntnose stingray		1		1	.9
Megalopidae					
Megalops atlantica, tarpon	2	1		3	2.7
Elopidae					
Elops saurus, ladyfish	2		3	5	2.7
Albulidae					
Albula vulpes, bonefish			4	4	3.6
Ophichthidae					
Myrophis punctatus, speckled worm eel			2	2	1.8
Clupeidae					
Harengula jaguana, scaled sardine	1,941	45,790	12,001	59,732	64.3
Sardinella anchovia, spanish sardine	170	107	27	304	17.0
Opisthonema oglinum, Atlantic thread herring	87	88	1	176	8.9
Brevoortia patronus, gulf menhaden	1,069	1,046	6,733	8,848	17.9
Etrumeus teres, round herring			1	1	.9
Engraulidae					
Anchoa lyolepis, dusky anchovy	6,855	41,690	15,486	64,031	47.3
A. hepsetus, striped anchovy	74	2,656	1,021	3,751	44.6
A. mitchilli, bay anchovy	788	275	1,890	2,953	29.5
A. cubana, cuban anchovy	5	2		7	1.8
Anchovialla perfasciata, flat anchovy	507	514	234	1,255	21.4
Synodontidae					
Synodus foetens, inshore lizard fish	26	30	11	67	18.8
Ariidae					
Arius felis, sea catfish	8	16	6	30	13.4
Gobiesocidae					
Gobiesox strumosus, skilletfish		3	10	13	5.4
Gadidae					
Urophycis regius, spotted hake			1	1	.9
Polynemidae					
Polydactylus octonemus, Atlantic threadfin			2	2	.9
Pomatomidae					
Pomatomus saltatrix, bluefish		11	28	39	8.0
Rachycentridae					
Rachycentron canadum, cobia		4		4	1.8
Sphyraenidae					
Sphyraena borealis, northern sennet		24	106	130	12.5
S. guachancho, guaguanche		7		7	3.6
Scombridae					
Scomberomorus maculatus, spanish mackerel	7	52	4	63	12.5
Lutjanidae					
Lutjanus sp., snapper		1		1	.9
Mugilidae					
Mugil cephalus, striped mullet	4	323	493	820	24.1
M. curema, white mullet	3	73	420	496	24.1
Stromateidae					
Peprilus sp., butterfish		2	1	3	1.8
Gerreidae					
Eucinostomus sp., mojarra	142	553	180	875	36.6
Sparidae					
Archosargus probatocephalus, sheepshead		2		2	1.8
Lagodon rhomboides, pinfish	27	7	1,216	1,250	18.8
Uranoscopidae					
Astroscopus y-graecum, southern stargazer		11	8	19	9.8

TABLE 2.—*Continued.*

Species	1975	1976	1977	Total	Frequency of occurrence
Pomacentridae					
Abudefduf saxatilis, sergeant major			18	18	.9
Lobotidae					
Lobotes surinamensis, tripletail	1	236	5	242	21.4
Blenniidae					
Hypsoblennius sp., blenny		22	2	24	6.3
Gobiidae					
Gobionellus hastatus, sharptail goby		1		1	.9
Ophidiidae					
Lepophidium sp., cusk eel		1		1	.9
Exocoetidae					
Hemiramphus brasiliensis, ballyhoo		3		3	1.8
Hyporhamphus unifasciatus, halfbeak	1	3	24	28	6.3
Belonidae					
Strongylura marina, Atlantic needlefish		3	1	4	1.8
Cyprinodontidae					
Fundulus similis, longnose killifish		2	2	4	3.6
Atherinidae					
Menidia beryllina, tidewater silverside	29	35	109	173	24.1
Membras martinica, rough silverside	180	5	317	502	17.9
Syngnathidae					
Syngnathus louisianae, chain pipefish	2	133	35	170	26.6
S. floridae, dusky pipefish	7	3	7	17	6.3
S. scovelli, gulf pipefish	5		2	7	2.7
Hippocampus zosterae, dwarf seahorse		1		1	.9
Sciaenidae					
Bairdiella chrysoura, silver perch		1	2	3	2.7
Cynoscion arenarius, sand seatrout		7		7	.9
C. nebulosus, spotted seatrout	1		2	3	2.7
Leiostomus xanthurus, spot	6	796	1,415	2,216	18.8
Menticirrhus littoralis, gulf kingfish	269	431	694	1,394	67.0
M. americanus, southern kingfish	19	213	40	272	25.9
M. saxatilis, king whiting	10	52	54	116	34.8
Larimus fasciatus, banded croaker		13	5	18	4.5
Micropogonias undulatus, Atlantic croaker		3		3	1.8
Carangidae					
Chloroscombrus chrysurus, Atlantic bumper	3	9	13	25	8.9
Trachinotus carolinus, Florida pompano	154	528	2,586	3,268	56.3
T. falcatus, permit		1		1	.9
Oligoplites saurus, leatherjacket	4	4	2	10	6.3
Caranx hippos, crevalle jack	2	56	14	72	11.6
Seriola zonata, banded rudderfish		1		1	.9
Selene vomer, lookdown		1		1	.9
Dactyloscopidae					
Dactyloscopus tridigitatus, sand stargazer			2	2	.9
Triglidae					
Prionotus tribulus, bighead searobin			1	1	.9
Cynoglossidae					
Symphurus plagiusa, blackcheek tonguefish		1		1	.9
Bothidae					
Citharichthys macrops, spotted whiff	3	16	4	23	6.3
Etropus sp., flounder		627	2	629	13.4
Paralichthys albigutta, gulf flounder		19	2	21	4.5
P. lethostigma, southern flounder	2	9	6	17	3.6
Tetraodontidae					
Sphoeroides sp., puffer		196	35	231	18.8
Balistidae					
Monacanthus hispidus, planehead filefish		39		39	4.5
Aluterus schoepfi, orange filefish		3		3	.9
Diodontidae					
Chilomycterus schoepfi, striped burrfish			1	1	.9
Totals	12,415	96,763	45,291	154,469	

Carangidae, and Sciaenidae. The dusky anchovy, *Anchoa lyolepis*, and the scaled sardine, *Harengula jaguana*, were numerically most important making up 80.2% of the total number of fishes collected. These species were abundant in all 3 yr, although *A. lyolepis* was most numerous in 1975 and 1977 and *H. jaguana* in 1976. The families Sciaenidae and Carangidae were represented by nine and seven species, respectively. The gulf kingfish, *Menticirrhus littoralis*, although only eighth in number, exhibited the highest frequency of occurrence (67%) of any species. The Florida pompano, *Trachinotus carolinus*, was the only carangid regularly occurring in the surf zone.

Relationships within two genera, *Sardinella* (Clupeidae) and *Menidia* (Atherinidae), are currently uncertain for the Gulf of Mexico. We followed Houde and Fore (1973) and Hoese and Moore

(1977) in recognizing the low anal ray count (generally 16) specimens of *Sardinella* sp. as Spanish sardine, *S. anchovia*. Our specimens of *Menidia* generally had three or fewer anal fin rays anterior to the posterior extension of the swim bladder by which Johnson (1975) characterized *M. peninsulae* (Goode and Bean). However, we have followed Edwards et al. (1978) in retaining tidewater silverside, *M. beryllina*, for this form.

Although some variation occurred in the annual ranking of species abundance (Table 3), *A. lyolepis*; *H. jaguana*; and gulf menhaden, *Brevoortia patronus*, were among the four most abundant species in all 3 yr. Less numerous species showed more variability. For instance, the striped anchovy, *A. hepsetus*, was third in abundance in 1976 but eighth in abundance in 1977, while *T. carolinus* was sixth in abundance in 1976 and fourth in abundance in 1977.

TABLE 3.—Rank order of abundance of the 10 most numerous fish species collected from the Horn Island, Miss., surf zone by year.

Species	1975	1976	1977
Anchoa lyolepsis	1	2	1
Harengula jaguana	2	1	2
Brevoortia patronus	3	4	3
Anchoa mitchilli	4	—	5
Anchoviella perfasciata	5	9	—
Menticirrhus littoralis	6	10	9
Membras martinica	7	—	—
Sardinella anchovia	8	—	—
Trachinotus carolinus	9	8	4
Eucinostomus sp.	10	7	—
Leiostomus xanthurus	—	5	6
Etropus sp.	—	6	—
Lagodon rhomboidas	—	—	7
Anchoa hepsetus	—	3	8
Mugil cephalus	—	—	10

The number of fishes collected from the surf zone habitat of Horn Island was characterized by distinct seasonal changes. Peaks in fish per seine haul (collected between 0900 and 1600 h) occurred during the warmer months between June and September 1976 and 1977 (Figure 2). In 1975 fishes were not collected in large numbers until the August collection. Large numbers of fishes were collected as early as June in 1976 although few fishes were collected in July of the same year. In 1977 fishes were not collected in abundance in June, but were in July.

The number of fishes collected dropped during the fall and winter months but rose again during late winter and early spring (Figure 2). This secondary peak, occurring in March 1976 and 1977, was composed of denatant migrants (sensu Cushing 1975) which had recently been spawned

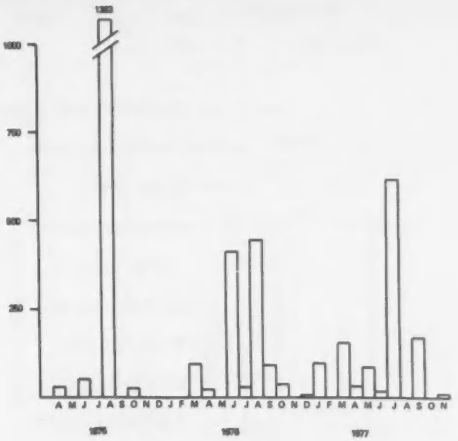

FIGURE 2.—Mean number of fishes collected per seine haul from Stations 1 through 4 on Horn Island, Miss., between April 1975 and November 1977. Data represents collections made between 0900 and 1600 h c.s.t.

offshore and were drifting into Mississippi Sound via the barrier island passes. Following the late winter (March) peak there was another period of low catch per effort between April and June in 1976 and 1977.

The numerically dominant species collected within the surf zone exhibited distinct seasonal occurrence patterns. Cluster analysis among these species indicated three modes of occurrence (Figure 3). Although data for the cluster analysis included only fishes collected between 0900 and 1600 h, there was no significant difference (χ^2, 5% level) in the monthly presence of fish species collected at this time period and those collected between 1600 and 0900 h. The most numerous species, *A. lyolepis* and *H. jaguana*, showed the highest similarity in seasonal occurrence and were most common during spring and summer. Other species also characteristic of spring and summer included *Eucinostomus* sp. and *T. carolinus*. *Anchoa hepsetus* and *Menticirrhus littoralis* had less seasonal affinity with the above species since they also occurred well into fall.

A second seasonal group included flat anchovy, *Anchoviella perfasciata*; *S. anchovia*; and white mullet, *Mugil curema*, which were representatives of the summer fauna (Figure 3). These species were never collected at water temperatures below 24.5° C.

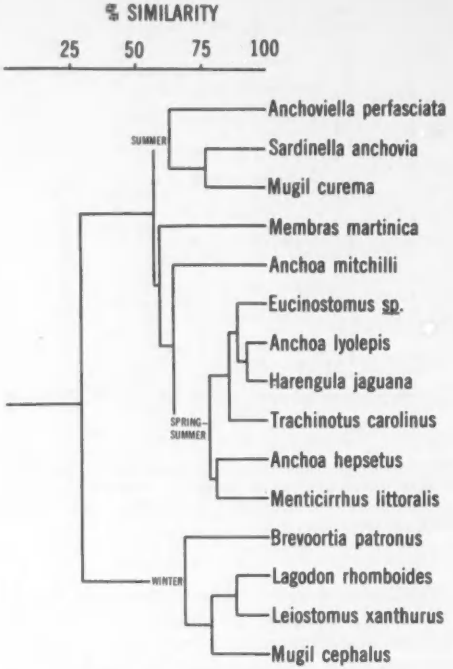

FIGURE 3.—Similarity dendrogram for species by month, based on presence or absence data, for fishes collected from the surf zone of Horn Island, Miss.

The third seasonal species group, *B. patronus*; pinfish, *Lagodon rhomboides*; spot, *Leiostomus xanthurus*; and striped mullet, *Mugil cephalus*, was prevalent during winter or early spring, generally in water temperatures below 24.5° C, with the first three occurring at temperatures as low as 11.5° C. Together these four species composed the secondary abundance peak of March 1976 and 1977 (cf. Figure 2).

Rough silverside, *Membras martinica*, and bay anchovy, *Anchoa mitchilli*, did not fit within the three seasonal categories. *Anchoa mitchilli* was collected in greatest abundance during the spring and in the fall, while *M. martinica* was most common in the spring, but only during 1975 and 1977. *Membras martinica* was infrequent in 1976.

Multiple regression analysis explained little of the variation associated with fish abundance (i.e., fish per seine haul). However, while tentative, the analysis may indicate the relative importance of these variables in controlling fish occurrence (Table 4). The dominant factor affecting the clupeiform fishes was tide level. Tide contributed only 5.1% and 8.9% in the regression equations for *H. jaguana* and *A. hepsetus*, and accounted for 19.2% of the model for *A. lyolepis* ($P<0.05$). The remaining variables contributed little to the predictive ability of the regression equations, although salinity composed 5.6% of the variance model for *A. hepsetus* ($P<0.05$). Temperature was the dominant parameter in the model for *T. carolinus* (not significant) and *Menticirrhus littoralis* ($P<0.05$).

While not apparent from Table 4, our observations indicate that catch per effort (cf. Figure 2) may coincide with wind direction. Wind patterns in the study area undergo annual cycles in which direction is primarily from the north during the winter and from the south during the summer. Fishes were collected in greatest numbers during the summer when southerly winds predominated.

Daily Activity Patterns

The greatest number of fishes were present within the surf zone during the early morning

TABLE 4.—Stepwise multiple regression of the five major environmental parameters contributing to the average number of fish collected per seine haul in the surf zone of Horn Island, Miss.

Species and parameter	Cumulative R	R^2	Cumulative R^2	F	df
Anchoa lyolepis					
Tide	0.438	0.192	0.192	15.72*	6, 75
Wave height	.452	.012	.205	.16	
Wind direction	.457	.005	.209	.23	
Temperature	.461	.003	.212	.22	
Wind speed	.462	.001	.213	.06	
Harengula jaguana					
Tide	.227	.051	.051	3.96*	5, 76
Temperature	.255	.014	.065	.82	
Wind direction	.274	.010	.075	.69	
Salinity	.278	.002	.077	.20	
Wave height	.279	.001	.078	.06	
Anchoa hepsetus					
Tide	.297	.089	.089	8.96*	6, 76
Salinity	.380	.056	.144	5.00*	
Temperature	.398	.014	.158	.90	
Wind direction	.411	.011	.169	1.00	
Slope	.415	.003	.172	.32	
Trachinotus carolinus					
Temperature	.199	.040	.040	2.14	7, 74
Salinity	.241	.018	.058	1.02	
Wind speed	.254	.007	.065	.93	
Tide	.262	.004	.068	.68	
Wind direction	.268	.004	.072	.60	
Menticirrhus littoralis					
Temperature	.309	.095	.095	8.62*	6, 75
Tide	.329	.013	.108	.77	
Salinity	.333	.002	.111	.21	
Wave height	.334	.001	.112	.52	
Slope	.338	.002	.113	.38	

*Significant ($P<0.05$).

(0300-0900) for all six 24-h samples made in 1976 (Figure 4). From May to September, excluding August when diel collections were not taken, fishes exhibited a distinct rise in abundance between 0300 and 0600 h c.s.t. with peak occurrences just after sunrise. The number of fishes collected during this time period far exceeded those captured during the later daylight hours; in June no collection was made during this time period.

The daily pattern of catch per effort reflected the numerical dominance of *H. jaguana* and *A. lyolepis*. The greatest number of fish for both species was collected during the early morning with a subsequent decline throughout the day (Figure 5). Peak capture rates for *H. jaguana* and *A. lyolepis* were 1,712 and 2,339 fish/seine haul, whereas the lowest mean rates were 6 and 0.1 fish/seine haul during the 1200-1500 h period for *H. jaguana* and the 1800-2100 h period for *A. lyolepis*. A secondary peak in abundance occurred between 1500 and

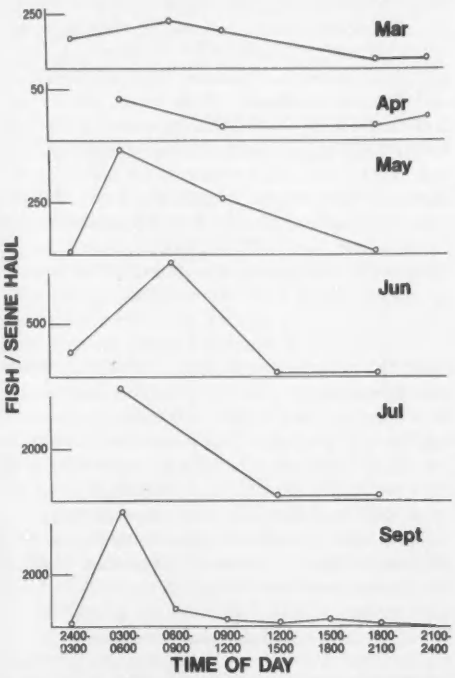

FIGURE 4.—Monthly mean number of fish per seine haul collected during the designated time intervals from the surf zone of Horn Island, Miss., between March and September 1976, excluding August.

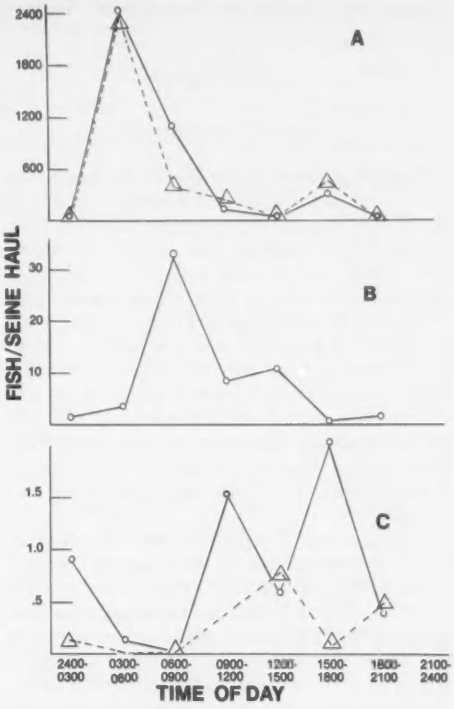

FIGURE 5.—Daily changes of mean number of fish per seine haul for the Horn Island, Miss., surf zone (April 1976-September 1976). Data are for the numerically most important species. A = *Anchoa lyolepis* (broken line) and *Harengula jaguana* (solid line). B = *Anchoa hepsetus*. C = *Trachinotus carolinus* (broken line) and *Menticirrhus littoralis* (solid line).

1800 h with 252 and 545 fish collected per seine haul for *H. jaguana* and *A. lyolepis*. High numbers of *A. hepsetus* also occurred during the morning; however, peak catch per effort occurred between 0600 and 0900 h. This species was less abundant than *H. jaguana* and *A. lyolepis*, with only 33 fish collected per seine haul. *Anchoa hepsetus* remained within the beach area through 1200-1500 h, but no fish were captured between 1500 and 1800 h.

Menticirrhus littoralis and *T. carolinus* did not exhibit distinct daily activity patterns, but tended to be more abundant during midafternoon or evening. The greatest number of *M. littoralis* collected was only 2.0 fish/seine haul between 1800 and 2100 h while the greatest number of

T. carolinus per seine haul was 0.8 fish between 1500 and 1800 h.

DISCUSSION

Species Composition

The ichthyofauna of the Horn Island surf zone resembles that of other surf zone habitats within the Gulf of Mexico. Using similar collecting gear, Gunter (1958) reported that over a 3-yr period *T. carolinus* and *H. pensacolae* (= *H. jaguana)* were the numerical dominants from the surf zone of Mustang Island, Texas. McFarland (1963), using a much larger seine (193 m long with 1.9 cm mesh), found that *Mugil cephalus* and Atlantic threadfin, *Polydactylus octonemus*, were dominant by weight and number, respectively, of the same area. While fishes collected by McFarland were generally >100 mm, many of the same species were collected by Gunter (1958) and in our study as larvae and juveniles.

Springer and Woodburn (1960) described a faunal assemblage for the surf habitat (exposed beach) near Tampa Bay, Fla., which was very similar to that of Horn Island. *Harengula jaguana* was the numerically dominant species collected during the warmer months, followed numerically by *Lagodon rhomboides* and *Menticirrhus littoralis*.

Although a numerically dominant species in the present study, *Anchoa lyolepis* has never been reported as common within a Gulf of Mexico coastal surf habitat. Gunter (1958) reported that *A. lyolepis* was taken only occasionally in the surf zone of Mustang Island, and Naughton and Saloman (1978) found it to be rare in a western Florida surf area. Springer and Woodburn (1960) collected only *A. hepsetus* and *A. mitchilli* from exposed beaches near Tampa Bay. Daly (1970) found *A. nasuta* (synonymized with *A. lyolepis* by Whitehead 1973) to be uncommon on the western tip of south Florida, although it ranges from Cape Hatteras, N.C., into the Gulf of Mexico through the West Indies to the Gulf of Venezuela (Daly 1970). In Mississippi Sound, Christmas and Waller (1973) occasionally collected *A. nasuta* of 36-59 mm SL in higher salinity water (20.0-35.5‰). Their data, based on several years of observation, indicated that *A. nasuta* occurred only in the summer and fall and was never abundant.

In comparing latitudinal variation of surf zone ichthyofaunas Gunter (1958) suggested that the major species occupying the Texas beach were the same or cognates to species observed in North Carolina which were cognates to those reported from New England beaches. Springer and Woodburn (1960) acknowledged that certain similarities existed within broad geographical ranges; however, they pointed out that many dissimilarities existed between temperate and tropical faunas within the eastern United States.

Between-study comparisons are made difficult due to differences in sizes of collecting gear and sampling designs. For instance, McFarland (1963) stated that the small clupeids, particularly the scaled sardine and engraulids, were undersampled because his collecting gear generally eliminated fishes <40 mm SL. However, for the warm-temperate to tropical regions of the Atlantic and Gulf of Mexico there seems to be a very characteristic species assemblage utilizing surf zone areas. Species listed as numerically important in both warm-temperate to tropical Gulf of Mexico and western Atlantic studies (Table 5) were *A. mitchilli*, *A. lyolepis* (= *A. nasuta*), *T. carolinus*, *M. littoralis*, and *H. jaguana* (= *H. pensacolae*). In addition, Atlantic silverside, *Menidia menidia*, and Atlantic menhaden, *B. tyrannus*, in the Atlantic and *M. beryllina* and *B. patronus* in the Gulf were numerically important. *Harengula jaguana* was most frequently reported as numerically dominant along Gulf of Mexico beaches; only Gilmore (1977) found it to have high abundance in the Atlantic surf zone off the Indian River area of Florida. However, the northern limit of this species is in the area of Cape Kennedy on the Florida Atlantic coast (Rivas 1963). Gilmore (1977) also found *A. nasuta* to be abundant in the surf zone along the eastern Florida coast. While *Menticirrhus littoralis* was not among the five most abundant species in some Gulf of Mexico studies (including ours), its high frequency of occurrence in our study indicates that it is an important surf zone species. Based on Table 5, atherinids, primarily of the genus *Menidia*, were more often among the five most abundant species collected in the Atlantic (seven out of nine studies) than Gulf of Mexico surf zones (two out of six studies).

Seasonal and Annual Variations

Temporal changes in both abundance and composition were primary characteristics of the ichthyofauna utilizing surf zone habitats of Horn Island. Fishes collected in our study were most

TABLE 5.—List of the first five numerically abundant fish species collected from the surf zone habitat of marine sandy beaches of the Gulf of Mexico and temperate Atlantic coast states.

Region	Major species	Total no. of species	Reference
Gulf coast:			
Mustang Island, Texas	*Trachinotus carolinus, Harengula jaguana, Mugil curema, Anchoa mitchilli, Micropogonias undulatus*	44	Gunter (1958)
Mustang Island, Texas	*Polydactylus octonemus, Menidia beryllina, Mugil cephalus, Menticirrhus littoralis, Chloroscombrus chrysurus*	48	McFarland (1963)
Gilchrist, Texas	*Brevoortia patronus,*[1] *Anchoa mitchilli, Polydactylus octonemus, Arius felis, Chloroscombrus chrysurus, Trachinotus carolinus*	25	Reid (1955b)
Horn Island, Miss.	*Anchoa lyolepis, Harengula jaguana, Brevoortia patronus, Anchoa hepsetus Trachinotus carolinus*	76	Present study
Panama City, Fla.	*Harengula jaguana, Menidia beryllina, Lagodon rhomboides, Trachinotus carolinus, Mugil curema*	44	Naughton and Saloman (1978)
Tampa Bay, Fla.	*Harengula jaguana, Lagodon rhomboides, Menticirrhus littoralis, Leiostomus xanthurus, Trachinotus carolinus*	47	Springer and Woodburn (1960)
East coast:			
Indian River, Fla.	*Harengula jaguana, Ophisthonema oglinum, Sardinella anchovia, Anchoa hepsetus, A. mitchilli, A. nasuta*[2]	78	Gilmore (1977)
Statewide, South Carolina	*Menidia menidia, Anchoa mitchilli, Trachinotus carolinus, Menticirrhus littoralis, Anchoa hepsetus*	39	Cupka (1972)
Folly Island, S.C.	*Menidia menidia, Anchoa hepsetus, Menticirrhus littoralis, Trachinotus carolinus, Mugil curema*	43	Anderson et al. (1977)
Beaufort, N.C.	*Menidia menidia, Anchoa mitchilli, Trachinotus carolinus, Menticirrhus* sp., *Fundulus majalis*	8	Pearse et al. (1942)
Beaufort, N.C.	*Brevoortia tyrannus, Anchoa hepsetus, Membras martinica, Lagodon rhomboides, Menticirrhus littoralis*	40	Tagatz and Dudley (1961)
Fire Island, N.Y.	*Sphoeroides maculatus, Alosa aestivalis, Poronotus triacanthus, Morone saxatilis, A. mediocris*	71	Schaefer (1967)
Long Island, Conn.	*Menidia menidia, Fundulus majalis, Menidia* sp. (immature), *Brevoortia tyrannus, Fundulus heteroclitus*	35	Hillman et al. (1977)
Pine Orchard, Conn.	*Menidia menidia, Sphoeroides maculatus, Brevoortia tyrannus, Pseudopleuronectes americanus, Syngnathus peckianus*	13	Merriman (1947)
Morris Cove, Conn.	*Menidia menidia, Brevoortia tyrannus, Syngnathus fuscus, Clupea harengus, Pseudopleuronectes americanus*	32	Warfel and Merriman (1944)

[1]Abundance of *Brevoortia patronus* was considered distorted due to the coincidence of a large school of adults moving inshore during the sampling effort.
[2]Equal numbers of *Anchoa mitchilli* and *A. nasuta* collected.

abundant during the summer, although the onset of high fish density varied somewhat between years. High numbers of fishes first appeared in June in 1976, but not until August in 1975 and July in 1977. Annual variability in the time of peak catch may be due, in part, to short-term variation in local water conditions. The low numbers of fishes collected in July 1976 may have been due to unusually calm and clear water which increased net avoidance. Large numbers of fishes were collected during the predawn hours of July 1976, indicating that fishes were abundant along the beach during this period.

Similar changes in the abundance of surf zone fishes have been observed in other studies. Gunter (1958) reported that fishes occupying the exposed beach of Mustang Island underwent seasonal succession during which fish abundance was greatest during the summer and least in the winter. Seasonal changes in abundance were also reported by Springer and Woodburn (1960), McFarland (1963), Schaefer (1967), and Anderson et al. (1977). McFarland (1963) proposed four categories of seasonal occurrence for surf zone fishes: all-year residents, spring-summer residents, summer residents, and winter residents. Of the major species common to both McFarland's study and ours, sea catfish, *Arius felis*; *Mugil cephalus*; and *L. rhomboides* were considered as all-year residents, whereas *H. jaguana*; *Anchoa* sp.; *T. carolinus*; *Menticirrhus littoralis*; king whiting, *M. saxatilis*; and southern kingfish, *M. americanus*, were classified as spring-summer residents. McFarland noted, as we have, that fishes characteristic of the spring and summer dominated the numerical component of the ichthyofauna.

The influx of denatant migrants collected within the surf zone during the winter in our study has not been reported previously. However, the annual movement of larval menhaden and sciaenids into estuaries along the Gulf of Mexico and Atlantic coasts during the winter is well documented (Gunter 1967; Dahlberg 1972; Christmas and Waller 1973). These species likely did not utilize the surf zone specifically, but were concentrated along the island before moving through the barrier island passes. Therefore, their appearance within the surf zone habitat appears dependent

more upon wind and current movements rather than habitat preference.

Throughout our study *A. lyolepis* and *H. jaguana* clearly dominated the numerical component of the surf zone ichthyofauna; however, differences in the rank of the remaining species did occur. Gunter (1958) suggested that intraseason species abundance in the surf zone of Mustang Island changed annually, although *T. carolinus* and *H. jaguana* were generally present in considerable numbers. Reid (1956) observed that the greater number of the surf zone ichthyofauna along the Texas coast, with the exception of *B. patronus*, was similar during successive summers. Star drum, *Stellifer lanceolatus*, was considerably more abundant during the second summer as were *T. carolinus*, *M. littoralis*, and *M. americanus*. During the first summer of a 3-yr study, Schaefer (1967) observed butterfish, *Peprilus triacanthus*, as the numerically dominant species within the surf zone of Fire Island, N.Y. In the remaining two summers of his study, northern puffer, *Sphoeroides maculatus*, was the most numerous species.

Factors Affecting Occurrence

The dominant factors affecting the abundance of fishes within the surf zone of Horn Island were tide level, time of day, and temperature. The frequency of engraulids and clupeids was closely associated with time and tide. However, during the summer sampling periods, when fish abundance was greatest in the early morning, tide levels were also highest. Consequently, the effect of the two factors is difficult to separate. Subsequent research (Ross unpubl. data) indicates that both may be important, although Roessler (1970) found that the frequency of *H. jaguana* collected from southern Florida was not significantly related to tidal fluctuation. Seasonal changes in temperature appeared to be of most importance in affecting the frequency of *T. carolinus* and *M. littoralis*.

The pronounced daily variation in occurrence of the most abundant fishes (i.e., *A. lyolepis*, *A. hepsetus*, and *H. jaguana*) indicates that they are not as permanently associated with the surf zone habitat as the gulf kingfish and the Florida pompano. Diel catch rates showed that engraulids and clupeids largely moved out of the surf zone during the day, whereas, the gulf kingfish and Florida pompano exhibited little change in daily abundance. Predator avoidance may be an important reason for the high early morning densities of the clupeoid fishes.

Other studies have also documented the influence of time of day and tidal cycle on fish abundance in surf areas. Merriman (1947) found that shore zone fishes in Connecticut had activity patterns associated with tide level. The greatest number of fishes occurred during high tide when fish appeared to be actively feeding. Daly (1970) also described daily activity patterns in anchovies collected along south Florida beaches. Anderson et al. (1977) suggested that temperature was the primary factor affecting fish abundance along a South Carolina beach; however, diel changes were not investigated. de Sylva et al. (footnote 3) also found that temperature was the greatest factor in determining frequency of most fishes, whereas salinity was secondary in importance and turbidity had little effect. The importance of temperature and salinity to the abundance and distribution of fishes has been discussed in depth by Gunter (1938, 1945, 1950, 1957) and to some extent by Warfel and Merriman (1944). Warfel and Merriman reported that the greatest and lowest number of fishes appeared relative to high and low temperatures, but that no direct correlation could be made. Gunter (1945, 1957) suggested that temperature was the dominant factor in initiating seasonal migrations and other cyclic activities of fishes along the Texas coast. The interaction of wind direction (i.e., inshore winds) with temperature may further increase the number of fishes in the Horn Island surf zone.

In summary, the Horn Island surf zone is utilized primarily by *H. jaguana*, *A. lyolepis*, *A. hepsetus*, *M. littoralis*, and *T. carolinus*. There is strong seasonal periodicity with the greatest abundance in spring and summer, as well as daily fluctuations due to tide level and time of day. Since the individuals of the above species were primarily late larval and juvenile forms, the importance of surf zone habitats as nursery and refuge areas for certain species should be recognized.

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LARVAL DEVELOPMENT OF PACIFIC TOMCOD, *MICROGADUS PROXIMUS*, IN THE NORTHEAST PACIFIC OCEAN WITH COMPARATIVE NOTES ON LARVAE OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, AND PACIFIC COD, *GADUS MACROCEPHALUS* (GADIDAE)

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ABSTRACT

A developmental series from yolk-sac larvae through juveniles (2.7-46.6 mm SL) of *Microgadus proximus* from the northeast Pacific Ocean is described and illustrated. Larvae hatch at approximately 2.7 mm SL and the yolk is absorbed by 3.0 mm SL. Notochord flexion begins between 8.0 and 10.0 mm SL, is completed at 15.0 mm SL, and transformation occurs between 22.0 and 28.0 mm SL. Larvae have specific pigment patterns, particularly in the postanal region where melanophores are arranged in two bars, anterior and posterior. At 5.0-6.0 mm SL, the anterior bar is located at 41-53% SL and the posterior bar is at 61-74% SL. Melanophore patterns on the head, gut, and caudal region also distinguish *M. proximus*. The occurrence of larvae taken within 18 km of shore off Oregon during plankton surveys in 1971-72 is discusssed, and data indicate a winter-spring spawning period.

A combination of pigmentation characters, primarily the length and position of the anterior and posterior pigment bars, and meristic counts can distinguish larvae of *M. proximus* from *Theragra chalcogramma* and *Gadus macrocephalus*. The anterior bar is located at 47-55% SL in *T. chalcogramma* and at 40-57% SL in *G. macrocephalus*. The posterior bar is located at 69-79% SL in *T. chalcogramma* and at 59-81% SL in *G. macrocephalus*. Both *T. chalcogramma* and *G. macrocephalus* have 4 rays on the superior hypural element while *M. proximus* has 5 rays. Other characters useful in separating the three species include head, gut, mediolateral, postanal, and caudal pigment and stripe continuity.

Problems have been encountered in distinguishing larvae of Pacific tomcod, *Microgadus proximus* (Girard); walleye pollock, *Theragra chalcogramma* (Pallas); and Pacific cod, *Gadus macrocephalus* (Tilesius), in samples from the northeastern Pacific Ocean where these three species might cooccur (Waldron 1972; Dunn and Naplin[3]). Larvae of *T. chalcogramma* were described by Gorbunova (1954) and Yusa (1954). Larvae of *G. (morhua) macrocephalus* larvae were described by Gorbunova (1954), Uchida et al. (1958), and Mukhacheva and Zviagina (1960). In this report we provide the first published description of the larvae of *M. proximus* and comparative material on larvae of *T. chalcogramma* and *G. macrocephalus* that should enable workers to identify larvae of these three gadids in mixed samples. Eggs and larvae of the Atlantic tomcod, *Microgadus tomcod*, were described by Booth (1967), but eggs of *M. proximus* are unknown.

The geographic range of *M. proximus* extends from off central California (Isaacson 1965) to the Gulf of Alaska and Unalaska Island (Wilimovsky 1964). Their presence in the Bering Sea remains unconfirmed, although they were reported to occur in the Bering Sea by Tanner (1894) and Hart (1973). *Microgadus proximus* was not captured in the eastern Bering Sea during extensive multivessel groundfish surveys in 1974 (Pereyra et al.[4]) or in 1976 (Bakkala and Smith[5]). *Microgadus proximus* is found from near-surface waters to ap-

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[3]Dunn, J. R., and N. A. Naplin. 1974. Fish eggs and larvae collected from waters adjacent to Kodiak Island, Alaska, during April and May, 1972. Unpubl. manuscr., 61 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[4]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Unpubl. manuscr., Vol. 1, 619 p.; Vol. 2, 534 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

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proximately 220 m (Miller and Lea 1972). Planktonic larvae of *M. proximus* were the dominant gadid and fourth most abundant taxon in a coastal assemblage of fish larvae occurring off Yaquina Bay, Oreg., in 1971-72 (Richardson and Pearcy 1977).

Information on the biology and taxonomy of *M. proximus* is limited. Schultz and Welander (1935) presented counts of meristic structures and morphological measurements of *M. proximus*. Svetovidov (1948), in his review of Gadiformes, provided some meristic data and a brief osteological description of *M. proximus* based on two skeletons. Brief notes on the biology of the species are included in Clemens and Wilby (1961), Miller and Lea (1972), and Hart (1973). It is not of commercial importance in part because of its small size (to 30 cm) but it is taken in recreational catches (Beardsley and Bond 1970; Hart 1973).

METHODS

Specimens

Several hundred larvae of the three species were examined in the course of this study. *Microgadus proximus* larvae and juveniles were obtained from plankton and trawl samples collected off Oregon in 1971-1973 and 1979, by the School of Oceanography, Oregon State University (OSU), Corvallis, and off Washington in 1972 by the Northwest and Alaska Fisheries Center (NWAFC). Additional specimens were obtained from plankton collected in Puget Sound, Wash., in 1977-79 by the Fisheries Research Institute (FRI), University of Washington, Seattle; and in 1978 by Ecology Consultants, Inc., Fort Collins, Colo. Larvae were also collected from near Kodiak Island, Alaska, in 1977-79 by FRI.

Theragra chalcogramma larvae were collected in the eastern Bering Sea (1971, 1976-78) and off Kodiak Island (1972, 1977-78) by NWAFC. Additional specimens from Puget Sound, Wash., (1977, 1978) were provided by FRI and by Ecology Consultants, Inc., and from off Kodiak Island (1978) by FRI.

Gadus macrocephalus larvae were collected near Kodiak Island in 1978 by NWAFC and FRI and from Puget Sound, Wash., in 1977-79 by FRI.

Radiographs were examined of juvenile and adult *M. proximus* and *G. macrocephalus* specimens in the collections in the Department of Fisheries and Wildlife, OSU, and NWAFC, and of adult *T. chalcogramma* specimens at NWAFC and from the Institute of Animal Resource Ecology, University of British Columbia, Vancouver.

Illustrations of larvae were made with the aid of a camera lucida. All specimens had been preserved in either 3-5% Formalin,[6] buffered with sodium borate, or 95% ethanol. Illustrations of caudal fin development were drawn from cleared and stained specimens.

Measurements

The following measurements were made on 72 unstained larvae and juveniles (2.7-46.6 mm SL) of *M. proximus* using an ocular micrometer in a stereomicroscope:

Standard length (SL)—Snout tip to notochord tip prior to development of caudal fin, then to posterior margin of hypural element. (All body lengths in this study are standard lengths.)

Head length (HL)—Snout tip to posterior edge of opercle (to pectoral fin base in yolk sac and very small larvae before opercular margin is visible).

Snout length—Snout tip to anterior margin of orbit of left eye.

Upper jaw length—Snout tip to posterior margin of maxillary.

Eye diameter—Greatest diameter of left orbit.

Body depth at pectoral—Vertical distance from dorsal to ventral body margin at pectoral fin base.

Body depth at anus—Vertical distance from dorsal to ventral body surface at center of anal opening.

Snout to anus—Distance along body midline from snout tip to vertical through center of anal opening.

Snout to first dorsal fin—Distance along the body midline to vertical through origin of anteriormost dorsal fin ray of first dorsal fin.

Snout to second dorsal fin—Distance along body midline to vertical through origin of anteriormost fin ray of second dorsal fin.

Snout to third dorsal fin—Distance along body midline to vertical through origin of anteriormost fin ray of third dorsal fin.

Snout to first anal fin—Distance along body midline to vertical through origin of anteriormost fin ray of first anal fin.

[6]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

Snout to second anal fin—Distance along body midline to vertical through origin of anteriormost fin ray of second anal fin.

Meristic Structures

Counts of meristic structures were made on 128 stained *M. proximus* larvae and juveniles. Sixty-six specimens (3.1-41.1 mm SL) were cleared and stained with Alizarin Red S (Taylor 1967), and 62 larvae (5.1-23.4 mm SL) were stained with Alizarin Red and Alcian Blue (Dingerkus and Uhler 1977). Both series of stained samples were used to make counts of meristic structures and to determine the onset and sequence of ossification as indicated by the uptake of Alizarin Red. Structures, including teeth, were considered ossified even if only slightly stained with Alizarin Red.

Counts on stained larvae and early juveniles were made of first, second, and third dorsal fin rays, first and second anal fin rays, caudal fin rays, left pectoral and pelvic fin rays, branchiostegal rays, gill rakers, abdominal and caudal vertebrae (including the postural centrum), and neural and haemal spines. Counts were made of premaxillary and dentary teeth on 12 specimens (11.9-41.1 mm SL).

Counts of meristic structures of juveniles and adults of *M. proximus*, *T. chalcogramma*, and *G. macrocephalus* were made from radiographs. Counts were made of first, second, and third dorsal fin rays, first and second anal fin rays, caudal fin rays, and abdominal and caudal vertebrae (including the postural centrum).

IDENTIFICATION OF *MICROGADUS PROXIMUS*

A developmental series of *M. proximus* specimens ranging from late yolk-sac larvae to early juveniles was linked by pigment patterns, myomere counts, fin development, and meristic counts in larger specimens. They were identified as gadids based on three criteria: 1) Distinctive pigment patterns, which in small larvae consist of an anterior and posterior pigment bar, each composed of a dorsal and ventral stripe. With further growth of larvae, these bars diffuse into dorso- and ventrolateral rows of pigment accompanied by development of a mediolateral line of melanophores. 2) Relatively high (54-58) myomere counts. 3) Presence of a "pseudocaudal" fin (Ahlstrom and Counts 1955) at about 8.5 mm SL, as indicated by the development of dorsal and ventral procurrent caudal rays before the development of hypurals.

Considering the collection locations (coastal Oregon and Washington) and the range of myomere counts, the specimens could have been one of only three potential species, *M. proximus*, *T. chalcogramma*, or *G. macrocephalus*. Meristic characters in the literature (e.g., Svetovidov 1948; Miller and Lea 1972; Hart 1973) are inadequate to separate all three species. Additional counts obtained in this study, particularly caudal vertebrae and fin rays on the superior hypural (Tables 1, 2), enabled positive identification of the series as *M. proximus*.

DEVELOPMENT OF *MICROGADUS PROXIMUS*

Pigment Patterns (Figures 1, 2)

Pigmentation varies in *M. proximus* larvae but basic trends persist and are useful in distinguishing the larvae. The importance of these pigment patterns is stressed by Russell (1976) for the entire family Gadidae. He feels many of the early larvae can be identified exclusively by specific pigment patterns. We follow his terminology by referring to the postanal pigment as bars according to their position, anterior and posterior. Russell's use of the term "bar" can be confusing, however, when referring to specific areas within a bar. We define bar as: anterior and posterior pigment area each composed of a dorsal and ventral stripe. Descriptions of pigment patterns for *M. proximus* are based primarily on 49 (2.7-31.0 mm SL) recently preserved (<2 yr) specimens in which fading was minimal.

Head Region

Pigment on the head of the smallest larvae (2.7-3.6 mm SL) is limited to a spot posterior to the pigmented eye and some melanophores on the lower jaw (Figure 1A). By 4.0 mm SL, 6 or 7 melanophores appear on the nape, 5 or 6 on the lower jaw, and a few internal as well as external melanophores on the forebrain. By 5.0 mm SL, added pigment occurs between the eyes, on both jaws and at the jaw angle, and internally, posterior to the eye (Figure 1B). Snout pigment appears at 8.0 mm SL (Figure 1C), and by 10.0 mm SL, pigment is added over the dorsal region of the head (Figure 1E). Pigment is added to these areas with

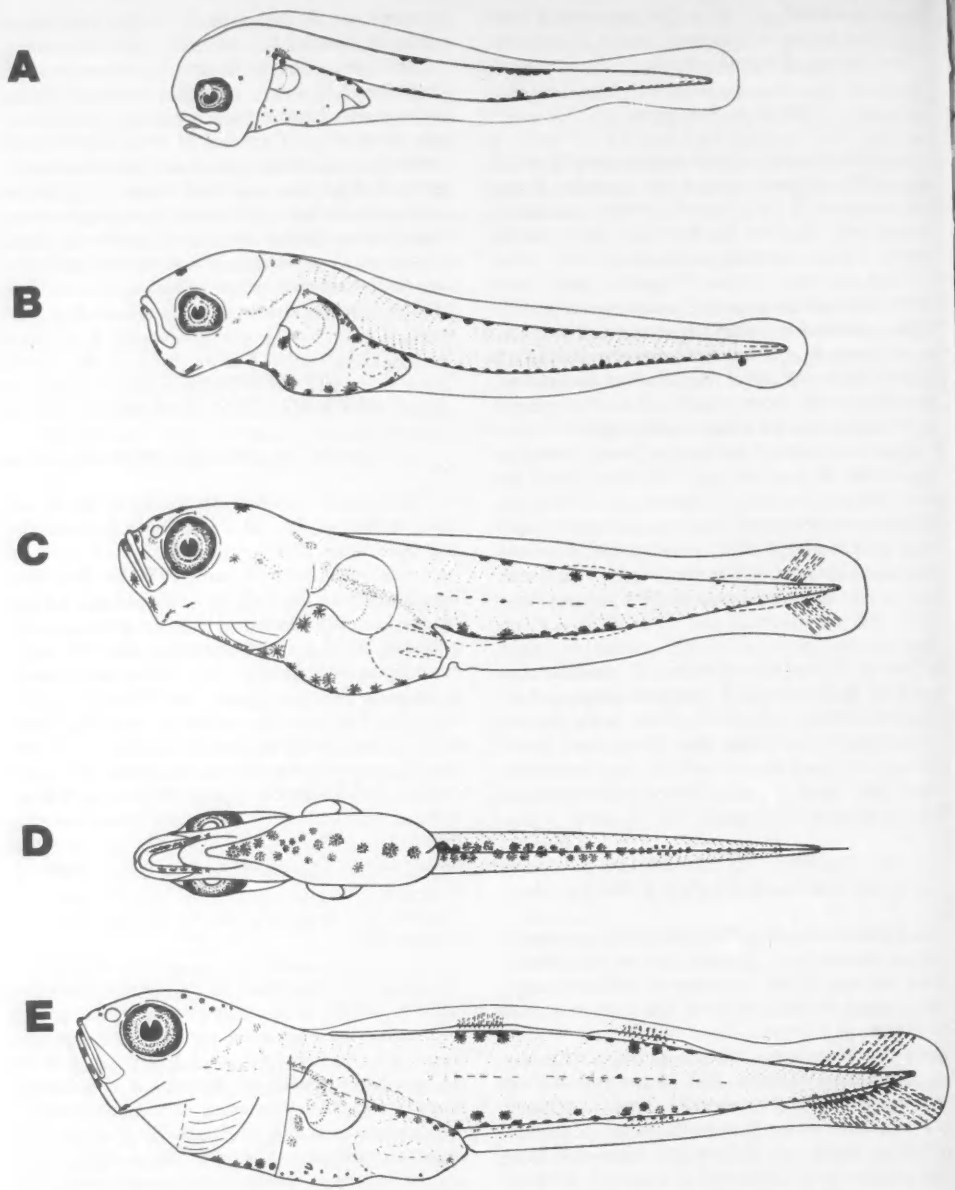


FIGURE 1.—Larval stages of *Microgadus proximus*: A. 3.6 mm SL; B. 5.7 mm SL; C. 8.4 mm SL; D. 8.4 mm SL (ventral view); E. 10.7 mm SL.

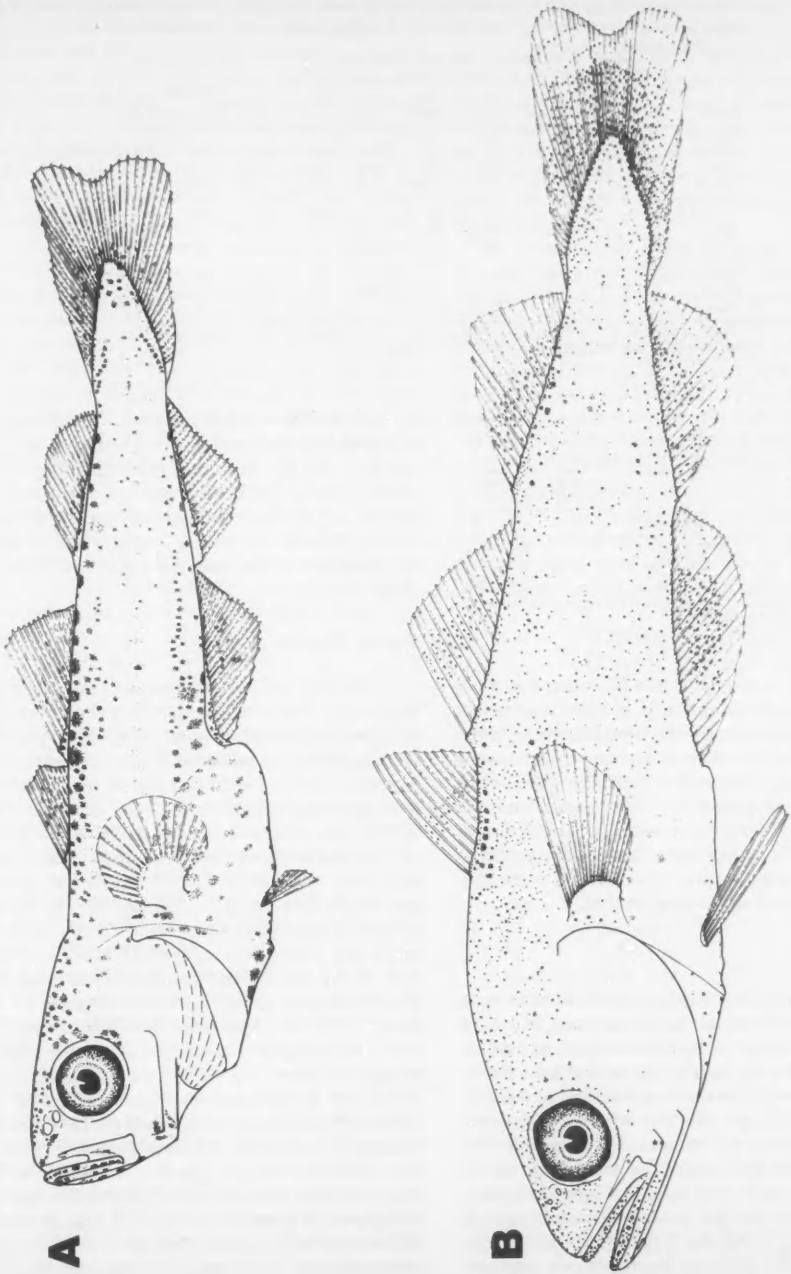


FIGURE 2.—*Microgadus proximus*: A. larva, 16.0 mm SL; B. early juvenile, 27.0 mm SL.

TABLE 1.—Summary of adult meristic counts for *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus*. Data for *T. chalcogramma* is after Wilimovsky et al. (1967)[1] except where noted.

Species	Fin rays					Vertebrae		
	First dorsal	Second dorsal	Third dorsal	First anal	Second anal	Total	Precaudal	Caudal
M. proximus:								
Sample size	37	38	39	38	38	38	38	38
Mean	12.8	18.8	20.7	25.2	22.9	55.7	19.3	36.4
Range	9-15	16-21	17-24	22-28	20-26	54-58	17-20	34-38
T. chalcogramma:								
Sample size	242	229	235	237	237	98	[2]49	[2]49
Mean	11.7	14.6	17.7	18.9	18.8	49.8	18.7	32.6
Range	10-14	12-18	15-21	16-22	16-23	48-52	18-20	31-34
G. macrocephalus:								
Sample size	40	41	42	42	41	40	40	40
Mean	12.4	15.6	15.4	19.7	17.2	53.2	19.9	33.3
Range	10-15	11-22	10-20	17-27	12-25	49-56	18-21	31-35

[1]From Wilimovsky, N. J., A. Peden, and L. Peppar. 1967. Systematics of six demersal fishes of the North Pacific Ocean. Fish. Res. Board Can., Tech. Rep. 34, 95 p.
[2]From this study.

TABLE 2.—Distribution of caudal rays on the superior hypural element in *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus* (Walters[1] and this study).

Species	No. of specimens	Percentage of caudal rays on superior hypural			
		3	4	5	6
M. proximus	1,335	0.0	8.0	92.0	<0.1
T. chalcogramma	241	0.0	99.0	1.0	0.0
G. macrocephalus	87	0.3	97.0	0.0	0.0

[1]G. E. Walters, College of Fisheries, University of Washington, Seattle, WA 98115, pers. commun. January 1979.

development, and by 16.0 mm SL it becomes more concentrated on the jaws, jaw angle, snout, between the eyes, and over the head extending to the nape (Figure 2A). Several melanophores appear ventrally along the median cartilage between the dentaries and urohyal. With transformation (completion of fin development) at 22.0-28.0 mm SL, small and densely concentrated melanophores are added to the jaws and dorsal head (Figure 2B). The opercular area is unpigmented.

Gut Region

Melanophores line the dorsal surface of the gut cavity in the smallest larva (2.7 mm SL), and several spots are on the ventral abdominal surface anteriorly. The isthmus is pigmented by 4.0 mm SL. Melanophores increase in number on the dorsal and ventral gut surface with development. Melanophores are added laterally, occurring first anteriorly near the base of the pectoral fin at 5.0 mm SL (Figure 1B). The melanophores on the ventral surface of the gut extend more posteriorly, forming a rough line nearly to the anus by 8.0 mm SL (Figure 1C, D). Gut pigmentation changes little through transformation, except for additional melanophores on the lateral surface (Figure 2A). In early juveniles, the lateral pigment is more internal than external and the overlying skin is unpigmented (Figure 2B). Along the ventral surface of the gut is a single row of small melanophores. The base of the pectoral fin is pigmented.

Postanal Region

Pigment in the postanal region is an important diagnostic character for *M. proximus* larvae. The smallest larvae (2.7-3.6 mm SL) have two pigment bars, anterior and posterior. The stripes within the pigment bars are double rows of melanophores with pigment on both sides of the body along the dorsal and ventral midline. At first, the dorsal stripes consist of only 1 or 2 melanophores on each side, but increase to 2 or 3 anteriorly and 6-8 posteriorly by 3.6 mm SL (Figure 1A). The ventral stripes on each side have 4 or 5 spots anteriorly and 7 or 8 spots posteriorly by 3.6 mm SL (Figure 1A). At 3.6 mm SL the anterior bar is located at 42-50% SL (myomeres 16-22) and the posterior bar is at 59-72% SL (myomeres 29-37). With development, melanophores are added along the ventral stripes between the bars, becoming continuous with them by 5.7 mm SL (Figure 1B). The two dorsal stripes remain separate until 15.0 mm SL, although occasionally a few melanophores may be seen between them. Pigment is added along the body midline, externally at 7.5 mm SL and internally at 9.5 mm SL (Figure 1C, E). Postanal pigmentation changes are minimal for larvae between 10.0 and 14.0 mm SL, except for the addi-

tion of some spots laterally and in the dorsal and anal fin folds. By 15.0-16.0 mm SL, additional melanophores occur along the dorsolateral and ventrolateral surface, but those in the bars remain enlarged and distinctive (Figure 2A). After transformation, the larval pigment bars are no longer visible and the entire lateral area is pigmented, as are the dorsal and anal fins (Figure 2B).

Posterior to the second pigment bar, melanophores occur in the caudal region along the ventral body margin in the smallest larvae, connect with the ventral stripes by 5.7 mm SL (Figure 1B), and extend to the notochord tip by 6.2 mm SL. Caudal melanophores are smaller and less dendritic than those in the bars and appear as a single ventral midline row (Figure 1D). Several melanophores are added on the dorsal body margin posterior to the second pigment bar by 10.0 mm SL and, eventually, to the caudal fin fold ventrally and posteriorly by 15.0 mm SL. By 16.0 mm SL the dorsal and ventral midlines are distinctively lined with melanophores, and the lateral midline pigment, both internal and external, extends to the tail tip (Figure 2A). The proximal portion of the caudal fin is pigmented. After transformation pigment covers most of the fin (Figure 2B).

Morphology (Tables 3, 4)

Larvae of *M. proximus* are moderately elongate with the greatest body depth, about 19% SL, occurring at or near the pectoral fin base. The body tapers slightly toward the anus and then narrows abruptly posterior to the anus. The gut is only moderately long. The distance from snout to anus ranges from 41% to 48% SL in larvae and declines to 45% SL in juveniles. In our smallest yolk-sac larva (2.7 mm SL), the vent opens laterally to the right near the ventral fin fold and does not become vertical until the larvae reach about 7.5-8.5 mm SL. This lateral position of the anus in small gadid larvae was reported by Marak (1967) and Russell (1976). All yolk is absorbed by 3.0 mm SL. Notochord flexion is protracted, beginning at about 8-10 mm SL and ending at about 15 mm SL. Transformation begins at about 22 mm SL and is completed at about 27-28 mm SL. The largest pelagic specimen collected was 46.6 mm SL.

Head length as a proportion of standard length increases from 22% SL in preflexion larvae to 32% SL in transforming specimens. It declines to 30% SL in pelagic juveniles. Eye diameter as a proportion of head length decreases from 35% HL in preflexion larvae to 25% HL in pelagic juveniles, whereas snout length/head length increases from 18% HL to 29% HL. Upper jaw length/head length and body depth at pectoral fin base/standard length remain relatively constant, increasing only slightly from preflexion larvae to the pelagic juvenile stage. Depth at anus/standard length increases from 11% SL in preflexion larvae to 19% SL in juveniles.

The distance from the snout to the origin of the first dorsal fin as a proportion of standard length decreases slightly during development while the distance from the snout to the second dorsal fin/standard length remains nearly constant. The length from the snout to the origin of the third dorsal fin/standard length increases slightly during development.

Distances from the snout to the origin of the first anal fin/standard length decreases slightly from 47% SL in larvae undergoing notochord flexion to 45% SL in pelagic juveniles, whereas the snout to second anal fin distance/standard length increases slightly from 63% SL in larvae undergoing notochord flexion to 68% SL in pelagic juveniles.

Meristic Structures (Tables 5, 6; Figure 3)

Considerable variation occurs in the development of meristic structures as the size at which bones ossify varies from specimen to specimen (Table 5). The following discussion approximately parallels the sequence of development of meristic characters in *M. proximus*. Terminology of bones follows Ahlstrom and Counts (1955) and Ahlstrom.[7]

Head and Axial Skeleton

Branchiostegals can be discerned in some specimens as small as 3.9 mm SL. Ossification begins in some larvae at 8.1 mm SL, but the full complement of seven branchiostegals is not consistently ossified until the larvae are about 19 mm SL. The sequence of ossification of branchiostegals is from upper to lower.

Teeth begin ossifying on the dentary in 11.9 mm SL larvae (Table 6). Initially, the number of teeth

[7]E. H. Ahlstrom, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. July 1979. (Deceased.)

TABLE 3.—Morphometric measurements, in millimeters, of larvae and juveniles of *Microgadus proximus*. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Head length	Eye diameter	Snout length	Upper jaw length	Depth at pectoral	Depth at anus	Snout to anus	Snout to first dorsal	Snout to second dorsal	Snout to third dorsal	Snout to first anal	Snout to second anal
2.7	0.6	0.2	0.1		0.5	0.3	1.0					
2.9	0.6	0.2	0.1		0.5	0.3	1.1					
3.4	0.7	0.3	0.1		0.4	0.3	1.4					
3.8	0.8	0.3	0.1		0.5	0.4	1.4					
4.1	0.8	0.3	0.1		0.6	0.4	1.7					
4.2	0.7	0.3	0.2	0.5	0.9	0.5	1.5					
4.5	1.2	0.3	0.1	0.3	1.1	0.5	1.9					
4.7	0.9	0.4	0.1	0.3	0.8	0.5	2.0					
5.1	1.2	0.4	0.2		0.9	0.6	2.3					
5.4	1.0	0.4	0.1		0.9	0.5	2.0					
5.5	1.2	0.4	0.2	0.3	1.0	0.5	2.4					
5.9	1.5	0.5	0.2	0.4	1.0	0.6	2.6					
6.1	1.5	0.5	0.3	0.4	1.1	0.7	2.4					
6.6	1.6	0.5	0.3	0.6	1.1	0.7	2.9					
6.9	1.4	0.5	0.4	0.6	1.2	0.8	2.6					
7.1	1.7	0.6	0.4	0.7	1.3	0.9	3.3					
7.3	1.8	0.5	0.4	0.7	1.3	0.9	3.1					
7.5	1.6	0.5	0.4	0.6	1.2	0.8	3.3					
7.9	1.7	0.6	0.4	0.6	1.3	0.9	3.4					
8.1	2.0	0.7	0.5	0.7	1.6	1.2	3.6					
8.3	2.1	0.7	0.6	0.9	1.6	1.2	3.6					
8.7	2.0	0.7	0.4	0.9	1.6	1.3	4.0					
8.9	2.3	0.7	0.6	0.8	1.6	1.3	4.1					
9.0	2.2	0.7	0.6	1.0	1.6	1.2	4.0					
9.2	2.2	0.7	0.6	1.0	1.7	1.2	4.0					
9.3	2.3	0.7	0.6	1.0	1.9	1.5	4.1	3.3	4.2	6.0		
9.6	2.2	0.7	0.6	0.9	1.8	1.4	4.4					
9.7	2.5	0.7	0.7	1.0	1.8	1.5	4.5					
10.1	3.0	0.8	0.9	1.2	2.1	1.9	4.8	3.6	4.8	6.7	4.9	6.7
10.2	2.2	0.8	0.6	1.0	1.8	1.4	4.4					
10.5	2.8	0.9	0.7	1.2	2.1	1.7	4.8	3.6	4.9		4.9	
10.8	2.9	0.9	0.7	1.2	2.1	1.7	4.6	3.7	4.9		4.7	
11.4	2.9	0.9	0.7	1.3	2.1	1.9	5.2	4.1	5.1		5.3	
11.7	2.8	0.9	0.8	1.2	2.1	1.9	5.1	3.9	5.2	7.4	5.2	
12.0	3.0	1.0	0.8	1.2	2.3	2.1	5.3	3.9	5.3	7.8	5.3	
12.5	3.4	1.0	0.8	1.2	2.5	2.2	5.8	4.5	6.0		6.0	
12.7	3.5	1.2	0.9	1.4	2.6	2.2	6.0	4.4	6.0	8.4	6.0	8.6
12.9	3.5	1.2	0.9	1.4	2.6	2.6	6.3	4.7	6.4	8.8	6.5	8.8
13.5	3.5	1.1	1.0	1.4	2.6	2.4	6.3	4.7	6.2	8.6	6.4	9.1
13.7	3.8	1.2	1.1	1.4	2.6	2.5	6.6	4.9	6.4	9.2	6.6	9.8
14.0	3.8	1.1	1.0	1.7	2.8	2.8	6.5	4.7	6.2	9.0	6.5	9.3
14.2	4.0	1.2	1.0	1.5	2.8	2.5	6.7	5.0	6.7	9.2	6.7	9.3
14.5	4.3	1.3	1.3	1.7	3.0	2.7	7.2	5.3	7.0	9.7	7.2	9.8
14.7	4.5	1.3	1.3	1.7	3.0	2.7	7.3	5.7	7.3	10.5	7.5	10.2
15.2	4.5	1.3	1.2	1.7	3.0	2.7	7.2	5.2	6.8	10.0	7.2	10.0
15.3	4.5	1.3	1.2	1.8	3.3	3.0	7.5	5.7	7.3	10.8	7.5	10.5
15.5	4.3	1.3	1.3	1.7	3.0	2.8	7.3	5.7	7.5	10.2	7.5	10.2
16.2	5.0	1.4	1.4	1.8	3.5	3.3	7.8	5.8	7.8	10.7	8.0	9.2
16.5	4.7	1.3	1.3	1.7	3.5	3.2	8.0	5.8	7.7	11.0	8.2	10.8
17.0	4.8	1.4	1.4	1.8	3.4	2.7	8.5	6.2	8.0	11.5	8.7	11.3
18.3	5.3	1.5	1.7	2.0	3.8	3.3	8.8	6.7	8.8	12.3	9.0	12.5
19.0	5.5	1.5	1.7	2.0	3.5	3.5	9.3	6.5	9.5	12.8	9.5	12.7
20.0	5.7	1.6	1.7	2.2	4.2	3.7	9.3	7.2	9.5	13.6	9.5	13.2
21.0	6.2	1.7	1.8	2.3	4.3	4.2	10.0	7.5	10.3	14.7	10.0	14.7
[1]22.1	6.1	1.8	1.7	2.7	4.7	4.3	10.5	7.8	10.8	15.3	10.5	14.8
[1]23.5	6.8	1.9	2.0	2.7	4.8	4.5	10.6	8.2	10.8	16.0	10.8	16.2
[1]24.0	8.2	1.9	2.0	2.8	5.2	4.7	11.3	8.5	11.5	16.2	11.5	16.3
[1]25.2	7.8	2.1	2.3	3.0	5.5	5.2	11.8	8.8	12.2	17.5	12.0	17.5
[1]26.3	9.5	2.2	2.5	3.2	5.5	5.5	12.5	9.2	12.2	18.0	12.5	18.2
[2]27.3	8.2	2.2	2.5	3.3	5.7	5.3	13.5	9.5	12.9	18.3	13.7	20.0
[2]28.0	8.7	2.3	2.5	3.5	6.0	5.7	14.3	9.7	13.2	19.7	14.8	20.6
[2]29.3	9.2	2.3	2.7	3.7	6.3	5.7	14.2	10.3	13.8	20.5	14.2	20.3
[2]31.3	9.5	2.5	2.8	3.8	6.3	5.7	14.2	11.2	14.7	21.7	14.3	20.8
[2]32.1	9.7	2.5	2.8	3.7	6.5	5.8	14.2	11.2	14.7	21.3	14.5	22.0
[2]34.3	10.8	2.5	2.8	4.0	7.5	7.2	15.3	11.7	16.0	22.8	15.8	23.3
[2]36.7	10.8	2.7	3.0	4.5	7.7	7.3	15.2	11.7	16.8	24.6	15.7	24.6
[2]38.0	10.8	3.0	3.2	4.5	7.8	7.5	16.5	12.8	17.5	25.5	16.5	25.8
[2]38.2	11.0	2.7	3.5	4.5	7.8	7.2	15.5	13.0	17.8	25.7	16.2	25.8
[2]40.1	11.7	2.8	3.5	4.7	7.9	7.2	16.7	12.8	18.0	26.0	17.0	26.3
[2]41.1	11.2	2.9	3.5	3.3	8.2	7.2	17.3	13.3	17.8	25.8	17.3	24.0
[2]41.3	12.5	3.0	3.8	5.0	8.3	8.2	18.3	14.0	19.0	27.8	18.0	27.3
[2]46.6	14.0	3.3	4.0	5.8	9.7	9.5	20.0	15.0	21.0	31.5	20.2	32.1

[1]Transforming.
[2]Pelagic juvenile.

TABLE 4.—Body proportions of larvae and juveniles of *Microgadus proximus*. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Preflexion	Flexion	Postflexion	Transforming	Pelagic juvenile
Sample size	[1]19	[2]25	10	5	13
Standard length (mm)	5.3±1.6 (3-8)	11.2±2.1 (8-15)	17.4±2.1(15-21)	24.2±1.6(22-26)	35.7±5.9(27-47)
Snout to anus length/SL	41.2±3.3 (36-47)	45.9±2.0(43-50)	48.1±1.0(47-50)	46.8±1.0(45-48)	44.6±3.3(41-51)
Head length/SL	21.9±2.6 (17-27)	26.0±2.2(22-31)	29.0±0.9(28-31)	31.6±3.6(28-36)	29.9±1.2(27-32)
Eye diameter/HL	35.1±5.0 (25-44)	31.6±2.3(27-36)	28.4±0.9(27-30)	26.1±2.8(23-30)	25.3±1.4(23-28)
Snout length/HL	17.8±7.0 (5-29)	28.6±2.3(20-30)	29.0±1.8(27-32)	27.5±2.2(24-30)	29.4±1.5(26-32)
Upper jaw length/HL	36.8±12.7(25-71)	40.9±3.4(35-46)	37.7±1.4(36-40)	38.1±4.4(34-44)	39.3±3.2(30-42)
Body depth at pectoral fin base/SL	17.3±2.7 (12-24)	19.3±1.0(18-21)	20.4±1.0(18-22)	21.2±0.6(20-22)	20.7±0.7(20-22)
Depth at anus/SL	10.8±1.1 (9-13)	16.5±2.0(13-20)	18.6±1.3(16-20)	20.0±0.7(19-21)	19.3±1.1(18-21)
Snout to first dorsal fin/SL		35.2±1.5(33-39)	35.8±1.0(34-37)	35.1±0.2 (35)	33.8±1.3(31-36)
Snout to second dorsal fin/SL		46.6±1.8(44-50)	47.7±1.4(45-50)	47.5±1.3(46-49)	46.1±1.1(43-47)
Snout to third dorsal fin/SL		66.0±2.3(63-71)	67.5±1.7(66-71)	68.5±0.8(68-69)	67.2±2.0(63-70)
Snout to first anal fin/SL		47.3±2.2(44-51)	48.9±1.2(47-51)	47.3±0.7(46-48)	45.3±3.4(42-53)
Snout to second anal fin/SL		62.5±1.6(19-72)	66.0±3.6(57-70)	68.5±1.0(67-69)	67.7±3.7(58-74)

[1]Sample size is 12 for upper jaw length.
[2]Sample size is 16 each for distances from snout to first dorsal fin and snout to second dorsal fin; 12 for distance from snout to third dorsal fin; 15 for distance from snout to first anal fin; and 9 for distance from snout to second anal fin.

on the dentary exceeds the number on the premaxilla, but this is reversed at about 23 mm SL with the difference increasing with growth. A similar change in number and location of teeth was reported to occur on the Pacific whiting, *Merluccius productus* (Ahlstrom and Counts 1955).

In larval and transforming specimens (11.9-22.3 mm SL), teeth are irregularly spaced and clustered in groups. Some are caninelike and others are recurved. As the larvae grow, the teeth become more closely spaced as the numbers of teeth increase and approach biserialization in 34.3 mm SL juveniles, similar to that described for Pacific whiting (Ahlstrom and Counts 1955).

Gill rakers begin ossifying at 9.6 mm SL and all (3 + 20 = 23) gill rakers are ossified in a 24.3 mm SL larva.

Neural spines in the abdominal region begin to ossify at about 8.7 mm SL and all are ossified by 11 or 12 mm SL. Ossification generally proceeds posteriorly. Neural spines of the caudal region also begin ossifying at about 8.7 mm SL but ossification is not complete until specimens are 17 mm SL. The neural and haemal spines of the third to sixth vertebrae preceding the postural centrum begin to accept alizarin stain before other neural spines in the caudal region. Haemal spines ossify in a sequence similar to neural abdominal spines; all spines are ossified by 17 mm SL. The last neural and haemal spines to ossify are those associated with the terminal preural vertebrae. These spines are broadly flattened and ossify simultaneously with other bones of the caudal complex, as discussed later (Figure 3).

Vertebral centra in both the abdominal and caudal regions begin to ossify at about 8.7 mm SL and ossification is completed by 11 mm SL and about 19 mm SL. Ossification proceeds from anterior to posterior.

Fins

Median and paired fins showed some variation in development, with fin rays first forming at different body lengths in individual specimens (Table 5). Fin formation occurs in the sequence: larval pectoral fins; caudal fin; first anal fin; second anal fin; third, second, and first dorsal fins (nearly simultaneously); pelvic fins; and pectoral fins with rays.

The pterygiophores supporting anal and dorsal fin rays begin ossifying at 23.4 mm SL and ossification is complete by 31.1 mm SL. Too few specimens were available to follow the sequence of ossification.

Larval pectoral fins are present in our smallest specimen (2.7 mm SL). They consist of a fleshy base and an undifferentiated membrane. They persist until rays begin differentiating late in the larval period.

The caudal fin of *M. proximus* is associated with a complex of 16 centra (2 ural and 14 preural centra), 14 neural and haemal spines, 2 epurals, 1 superior hypural (HY 4-6), and 2 inferior hypurals (HY 2-3, HY 1) (Figure 3).

Caudal rays total 49-56, of which 22-25 are dorsal in origin, 22-26 are ventral in origin, and five are normally supported by the superior hypural. Principal caudal rays number 32-33; of these, 12 or 13 are dorsal in origin and 13 or 14 are ventral in origin. One each is attached to the two epurals, five are carried on the superior hypural, two on hypural 2-3, and one on hypural 1.

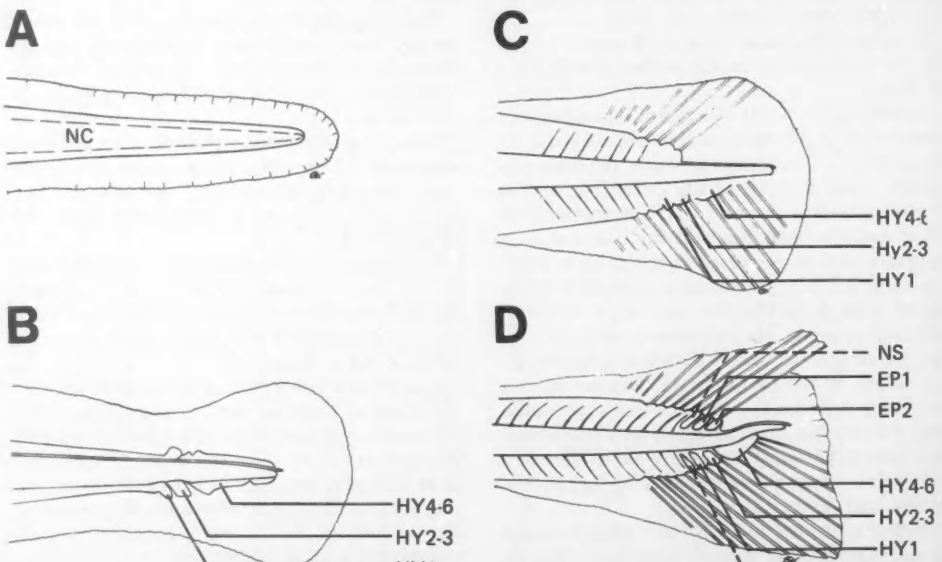
As with the Pacific whiting (Ahlstrom

and Counts 1955), some of the anterior caudal rays, both dorsally and ventrally, articulate with unmodified neural and haemal spines; other rays lie between the spines with no basal supports (Figure 3).

A symmetrical fin fold surrounds the tip of the notochord in specimens 3.1-5.5 mm SL (Figure 3). In 7.5 mm SL larvae, mesenchymal thickenings occur dorsal and ventral to the notochord. By 7.8 mm SL, the ventral thickening is differentiated into three cartilaginous plates constituting hypurals 1, 2, and 3 anteriorly, and hypurals 4-6 posteriorly (Figure 3B). In 9.5 mm SL specimens fin rays are considerably increased in number (Figure 3C). In 10.5 mm SL specimens the urostyle begins to flex, and the unossified hypurals 1, 2-3, and 4-6, as well as epurals 1 and 2 are differentiated (Figure 3D). Ossification proceeds rapidly during notochord flexion from anterior to posterior regions of the caudal complex. By 11.9 mm SL (Figure 3E), all preural centra are ossified, and all hypurals and both epurals have begun ossifying. Caudal fin rays have begun ossifying, beginning ventrally in the region of the inferior hypurals.

By 15.0 mm SL, all centra except the postural centrum are ossified; the hypurals and epurals are incompletely ossified (Figure 3F). Rays continue ossifying, proceeding posteriorly on the ventral margin and on the superior hypural and progressing anteriorly from epural number 2. By 19.4 mm SL all caudal rays posterior to preural centrum 12 are ossified. By 25.0 mm, the caudal fin is completely ossified (Figure 3G) and resembles in all details that of a 41.1 mm SL juvenile (Figure 3H).

We were unable to detect fusion of hypurals in the caudal fin of *M. proximus* during ontogeny. In the smallest larvae in which we could detect development of hypural elements (7.8-8.1 mm SL), only three hypurals could be observed. We believe, however, that these hypurals represent 1) an anterior, inferior hypural 1 (parhypural); 2) an inferior hypural representing a fusion of hypurals 2 and 3; and 3) a superior hypural representing a fusion of hypurals 4-6. This reasoning is predicated on 1) it is generally accepted that the evolutionary trend in fishes is toward a reduction in the number of hypurals, presumably by fusion of the constituent elements (Gosline 1961; Rosen and Patterson 1969; Marshall and Cohen 1973); 2) members of the family Moridae, generally considered a more primitive family than Gadidae (Svetovidov 1948; Greenwood et al. 1966; Rosen and Patterson 1969), possess three inferior and



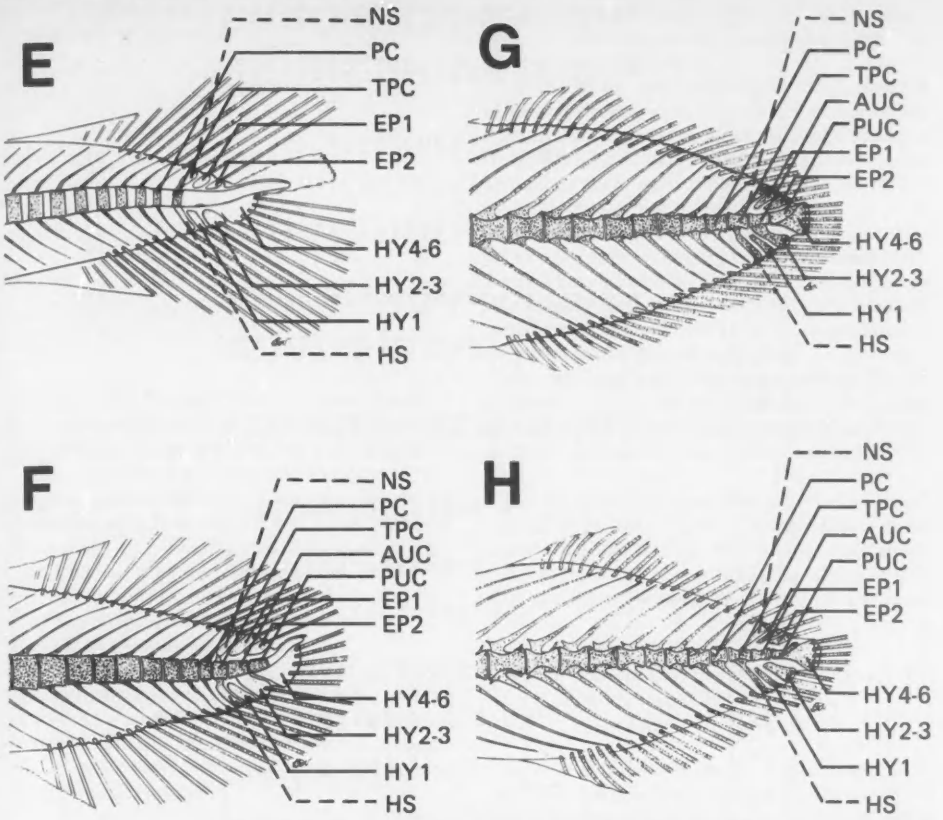


FIGURE 3.—Development of the caudal fin of *Microgadus proximus*: A. 5.2 mm SL; B. 7.8 mm SL; C. 9.5 mm SL; D. 10.5 mm SL; E. 11.9 mm SL; F.15.8 mm SL; G. 25.0 mm SL; H. 41.1 mm SL. AUC = anterior ural centrum; EP = epural; HS = haemal spine; HY = hypural; NC = notocord; NS = neural spine; PC = preural centrum; PUC = postural centrum; TPC = terminal preural centrum. Ossified elements are stippled.

three superior hypurals (Fitch and Barker 1972); and 3) presumably more advanced families of fishes in the same evolutionary line as gadids (e.g., order Batrachoidiformes) have two hypurals, apparently representing fusion of component parts (Rosen and Patterson 1969).

Barrington (1937), who figured and described the development of the caudal fin in *G. morhua*, provides the only other description of caudal development in gadids. His illustrations also depict only three hypural elements. Barrington, however, considered it unlikely that fusion of hypural bones could occur without some evidence of compound origin remaining in the fused bones. Our terminology of the caudal fin bones differs from that used by Barrington (1937) for *G. morhua*. We consider his ventral radial as hypural 1 and his dorsal radials 1 and 2 to be epurals 1 and 2.

Also we found no evidence of a uroneural in the development of the caudal fin of *M. proximus*. Rosen and Patterson (1969) consider the presence of one uroneural as a characteristic of the Gadiformes.

An anlage of the first anal fin is evident by 8.7 mm SL and the base of the second anal fin is present at 9.3 mm SL. Rays in the first anal fin begin ossifying at about 11.9 mm SL and in the second anal fin at 12.7 mm SL. Ossification is

TABLE 5.—Meristic counts from larval and juvenile *Microgadus proximus*. Values given are means. Specimens between dashed lines are undergoing notochord flexion.

Length interval (mm SL)	Sample size	Dorsal fin rays			Anal fin rays		Pectoral fin rays	Pelvic fin rays	Branchiostegal rays	Gill rakers			Neural spines			Haemal spines	Centra		
		First	Second	Third	First	Second				Upper	Lower	Total	Abdominal	Caudal	Total		Abdominal	Caudal	Total
3.0- 3.9	5																		
4.0- 4.9	3																		
5.0- 5.9	6																		
6.0- 6.9	9																		
7.0- 7.9	10																		
8.0- 8.9	13								1.1				3.2	2.8	6.0	2.9	2.5	2.7	5.2
9.0- 9.9	14								1.2		1.2	1.2	5.8	7.4	13.2	7.9	5.4	7.3	12.7
10.0-10.9	16								3.0		1.0	1.0	10.6	11.5	22.1	11.3	11.6	10.6	22.2
11.0-11.9	4				4.8				4.5		1.5	1.5	19.3	24.3	43.6	24.5	19.3	27.0	46.3
12.0-12.9	8		0.8	0.6	2.9	1.0			5.0		5.6	5.6	19.1	28.1	47.2	29.0	19.1	29.0	48.1
13.0-13.9	[1]4	0.8	2.5	2.8	3.0	2.3			5.8		16.5	16.5	19.3	26.5	45.8	26.0	19.2	25.8	45.0
14.0-14.9	4	1.3	3.0	1.3	7.5	2.5		2.2	6.3				19.5	35.0	54.5	34.0	19.5	33.0	52.5
15.0-15.9	[2]4	1.3	4.3	2.8	4.5		1.3	0.5	6.5		6.5	6.5	19.5	32.3	51.8	31.0	19.5	31.8	51.3
16.0-16.9	3	1.3	1.3		3.7				6.3				18.7	21.0	39.7	19.3	18.7	28.0	46.7
17.0-17.9	[3]3	5.0	9.0	10.0	18.0	13.7	7.0	4.0	7.0	0.3	16.3	16.6	19.3	35.3	54.6	35.0	19.3	37.0	56.3
18.0-18.9	3	4.3	9.7	10.3	12.0	12.7	9.3	3.0	6.7	0.3	16.7	17.0	19.0	33.7	52.7	33.7	19.0	31.3	50.3
19.0-19.9	2	5.5	13.0	8.0	18.0	14.5	6.5	2.5	7.0	0.5	16.0	16.5	19.5	33.5	53.0	32.5	19.5	35.5	55.0
20.0-20.9	1	6.0	6.0		14.0	10.0			7.0	1.0	17.0	18.0	20.0	35.0	55.0	34.0	19.0	37.0	56.0
21.0-21.9	1	7.0	11.0	13.0	17.0	12.0			7.0	1.0	16.0	17.0	19.0	35.0	54.0	34.0	19.0	36.0	55.0
22.0-22.9	2	10.5	16.5	14.5	22.5	17.0	8.5	5.5	7.0	1.0	19.0	20.0	19.0	34.5	53.5	34.5	19.0	37.0	56.0
23.0-23.9	2	11.0	20.0	20.0	26.0	22.5	18.0	6.0	7.0	2.5	19.5	22.0	19.0	34.5	53.5	34.5	19.0	36.5	55.5
24.0-24.9	1	13.0	19.0	21.0	26.0	24.0	17.0	5.0	7.0	3.0	20.0	23.0	19.0	34.0	53.0	34.0	19.0	37.0	56.0
25.0-25.9	1	12.0	19.0	15.0	24.0	16.0	3.0	5.0	7.0	3.0	19.0	22.0	19.0	36.0	55.0	36.0	19.0	38.0	57.0
26.0-26.9	1	13.0	23.0	20.0	28.0	17.0	17.0	6.0	7.0	3.0	20.0	23.0	19.0	34.0	53.0	35.0	19.0	37.0	56.0
28.0-28.9	1	12.0	21.0	21.0	28.0	24.0	19.0	6.0	7.0	3.0	19.0	22.0	17.0	34.0	51.0	34.0	17.0	37.0	54.0
29.0-29.9	1	13.0	21.0	21.0	28.0	23.0	17.0	6.0	7.0	3.0	18.0	21.0	19.0	33.0	52.0	33.0	19.0	36.0	55.0
30.0-30.9	1	13.0	20.0	22.0	26.0	24.0	18.0	6.0	7.0	4.0	24.0	28.0	20.0	33.0	53.0	33.0	20.0	36.0	56.0
31.0-31.9	1	13.0	17.0	22.0	25.0	25.0	19.0	6.0	7.0	4.0	21.0	25.0	19.0	34.0	53.0	34.0	19.0	37.0	56.0
34.0-34.9	1	12.0	20.0	22.0	25.0	23.0	19.0	6.0	7.0	4.0	22.0	26.0	18.0	34.0	52.0	34.0	18.0	37.0	55.0
38.0-38.9	2	13.5	18.0	21.0	24.0	26.0	19.5	6.0	6.5	—	—	—	19.5	33.0	52.5	33.0	19.5	36.0	55.5
41.0-41.9	1	13.0	20.0	22.0	26.0	22.0	18.0	7.0	7.0	4.0	21.0	25.0	20.0	33.0	53.0	33.0	20.0	36.0	56.0

[1]Sample size is 3 for pectoral and pelvic fins.
[2]Sample size is 2 for second anal fin.
[3]Sample size is 2 for second dorsal fin and pectoral fin.

TABLE 6.—Numbers of teeth on premaxillary and dentary bones in selected sizes of larval and juvenile *Microgadus proximus*.

Size of specimen (mm SL)	Teeth on left side	
	Premaxilla	Dentary
Larvae:		
11.9	0	1
13.2	0	6
15.0	0	6
15.8	0	6
17.2	8	10
18.0	6	8
Transforming:		
22.3	10	14
23.4	30	24
24.3	32	27
Juveniles:		
28.6	36	24
34.3	44	35
41.1	49	38

complete in the first anal fin at 23.0 mm SL and in the second anal fin at 27 or 28 mm SL. Ray development within a fin proceeds anterior to posterior.

Dorsal fins develop in a manner analogous to the anal fins and the three dorsal fins develop almost simultaneously. Dorsal fins 2 and 3 commence ossification at 12.9 mm SL, and dorsal fin 1 begins accepting stain at 13.2 mm SL. Ossification is complete in the first and second dorsal fins at 22.0 mm SL and in the third dorsal at 28.0 mm SL. Rays ossify from anterior to posterior.

Pelvic buds appear at about 8.0 mm SL. Pelvic fins begin ossifying at about 14.0 mm SL and are consistently ossified in 26.0 mm SL early juveniles. Pectoral fins initiate ossification at 15.0 mm SL and reach their full complement of 18-20 rays in 28.0 mm SL juveniles.

Scales

Scales begin developing in the anterior portion of the body near the dorsal tip of the cleithrum in 28.6 mm SL specimens. Development appears to progress along the lateral line as the juveniles grow. Scale development was not complete in our largest specimen, 41.1 mm SL.

Occurrence of *Microgadus proximus* (Figure 4)

Although a number of ichthyoplankton studies have been conducted in the northeastern Pacific Ocean, data on occurrence of *M. proximus* are limited because of past difficulties in distinguishing the larvae from other gadids. Larvae of this species may be included under the broader category of Gadidae listed in some papers (e.g., Waldron 1972; Pearcy and Meyers 1974). Some data on distribution and seasonal abundance, however, are available.

Larvae of *M. proximus* are found in coastal waters off Oregon occurring mainly within 18 km of shore with abundance peaks at about 6 and 9 km (Richardson and Pearcy 1977; Richardson[8]). A few specimens have been reported as far as 74 km offshore (Richardson footnote 8).

The larvae have been collected in the plankton off Oregon from February through August with peak abundance from March through July (Richardson footnote 8). Misitano (1977) also collected four specimens, 5-61 mm SL, from March to July in the Columbia River mouth.

Monthly length frequencies and median lengths of larvae collected in 1971 and 1972 off Oregon indicate a winter-spring spawning period (Figure 4). Small larvae, ≤5 mm SL, were collected February through June.

Larvae of *M. proximus* were collected 24 km off coastal Washington (Cruise K-72-2-III) in early June 1972, by the NWAFC[9]. This species accounted for 22.2% of the total catch of fish larvae, and specimens ranged from 5.0 to 26.0 mm SL.

COMPARATIVE NOTES ON *THERAGRA CHALCOGRAMMA* AND *GADUS MACROCEPHALUS* (Figure 5, Table 7)

In the northeastern Pacific Ocean, larvae of *M. proximus* are similar to those of *T. chalcogramma* and *G. macrocephalus* at sizes <16.0 mm SL. Identification of all three species in mixed samples is difficult with previously available literature, which describes *T. chalcogramma* and *G. macrocephalus* from the northwestern Pacific Ocean (e.g., Gorbunova 1954; Uchida et al. 1958; Mukhacheva and Zviagina 1960). We have summarized characters which are useful to distinguish each species at sizes <16.0 mm SL based on our examination of specimens of all three species (Table 7).

The most useful character to separate the smaller larvae (hatching to 10.0 mm SL) of the

[8]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution, and seasonality January 1971 to August 1972. Oregon State Univ., Sea Grant Coll. Program Publ. ORES-T-77-003, 73 p.

[9]Data on file for Cruise K-72-2 (III), 1972. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

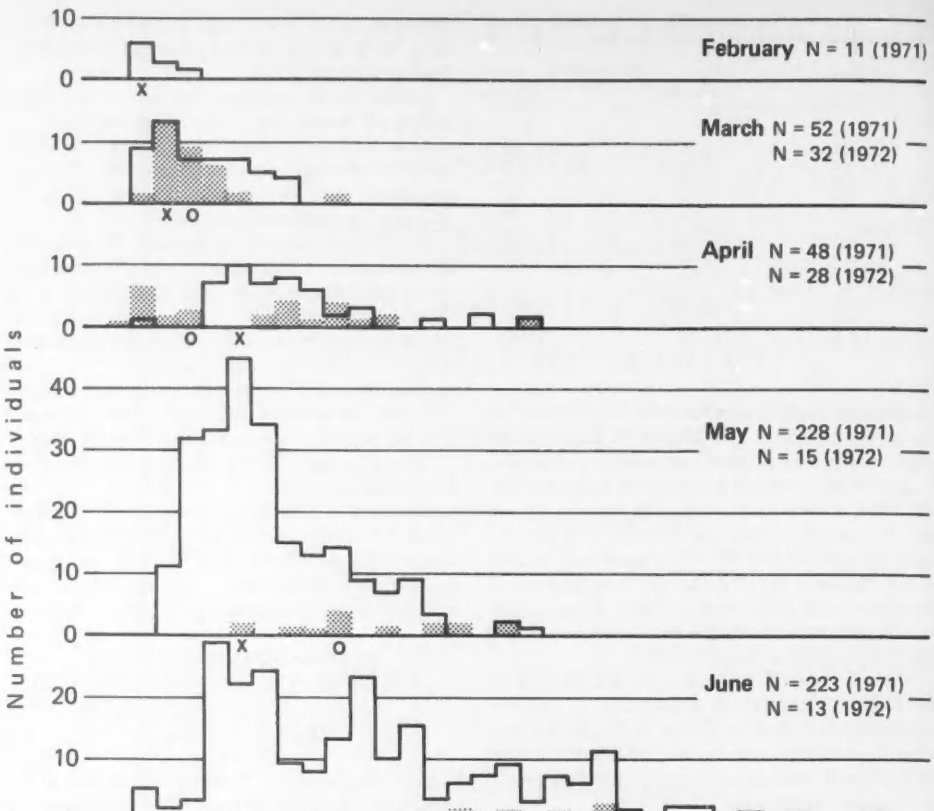

February N = 11 (1971)
March N = 52 (1971)
N = 32 (1972)
April N = 48 (1971)
N = 28 (1972)
May N = 228 (1971)
N = 15 (1972)
June N = 223 (1971)
N = 13 (1972)
July N = 103 (1971)
N = 5 (1972)
August N = 7 (1971)
N = 3 (1972)
Number of individuals
Length class (mm)

FIGURE 4.—Length-frequency histograms of *Microgadus proximus* larvae collected in 70 cm bongo nets off Oregon in 1971 (unshaded) and 1972 (shaded). X = median length class of larvae in 1971; O = median length class of larvae in 1972.

three species is the length and position of the anterior and posterior postanal pigment bars. In *M. proximus* larvae 5.0-6.0 mm SL (Figure 1B), the anterior bar begins just posterior to the anus at 41-53% SL (myomeres 14-23) and the posterior bar is at 61-74% SL (myomeres 28-39). In *T. chalcogramma* larvae of the same size range (Figure 5A), the anterior bar begins posterior to the anus at

47-55% SL (myomeres 21-26) and the posterior bar is at 69-79% SL (myomeres 36-43). The anterior bar begins posterior to the anus for similar size *G. macrocephalus* larvae (Figure 5C) at 40-57% SL (myomeres 16-26) and the posterior bar is at 59-81% SL (myomeres 26-42). Differences also exist in the number of melanophores in the stripe within a bar and associated bar length. This latter character, however, is only useful at small sizes (2.5-4.5 mm SL) because melanophores increase with development and the stripes become continuous. At 3.6 mm SL (Figure 1A), *M. proximus* larvae have on each side two dorsal and four ventral melanophores in the stripes within the small anterior bar, and seven melanophores each in the longer dorsal and ventral stripes within the posterior bar. Similar sized *T. chalcogramma* larvae (4.1 mm SL) have evenly sized stripes with five melanophores on both the dorsal and ventral stripe of the anterior bar, and five dorsal and seven ventral melanophores in each stripe of the posterior bar. *Gadus macrocephalus* larvae (4.4 mm SL) have longer stripes than the other two species, with 7 dorsal and 8 ventral melanophores on the anterior bar, and 11 dorsal and 10 ventral melanophores on the posterior bar.

With development these pigment stripes within the bars variously remain separate or become connected depending on the species. In *M. proximus* larvae the ventral stripes become continuous at 5.0-6.0 mm SL (Figure 1B) while the dorsal stripes remain separate until 13.0 mm SL. The dorsal stripes become continuous in *T. chalcogramma* larvae at 13.0 mm SL whereas the ventral stripes never connect. *Gadus macrocephalus* larvae have continuous dorsal and ventral stripes of melanophores by 5.0-6.0 mm SL (Figure 5C).

Other pigment differences may help in distinguishing species at certain size ranges. Early *G. macrocephalus* larvae (4.0-8.0 mm SL) have more head pigmentation than the other two species, particularly on the dorsal surface and in the snout area (Figure 5C). *Theragra chalcogramma* larvae (<13.0 mm SL) have much less lateral pigment on the surface of the gut than either *M. proximus* or *G. macrocephalus* larvae (Figure 5B). *Gadus macrocephalus* larvae (5.0-8.0 mm SL) have more mediolateral pigmentation between the postanal bars than the other two species in that size range (Figure 5C). Caudal pigment also differs and at sizes <10.0 mm SL can separate *M. proximus*. Only *M. proximus* larvae have a single row of ventral caudal melanophores posterior to the anal fin (Figure 1D) whereas both *T. chalcogramma* and *G. macrocephalus* larvae have isolated pigment spots (Figure 5B, D).

Also helpful in distinguishing *M. proximus* larvae from the other two species is the possession of five rays on the superior hypural compared with four rays for *T. chalcogramma* and *G. mac-*

TABLE 7.—Characters useful in separating larvae of *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus* at specific size ranges.

Character	Size range (mm)	*Microgadus proximus*	*Theragra chalcogramma*	*Gadus macrocephalus*
Anterior pigment bar	5-6			
Percentage of SL		41-53	47-55	40-57
Located at myomeres		14-23	21-26	16-26
Posterior pigment bar	5-6			
Percentage of SL		61-74	69-79	59-81
Located at myomeres		28-39	36-43	26-42
Number of melanophores in each stripe of:				
Anterior bar	3-4			
Dorsal		2	5	7
Ventral		4	5	8
Posterior bar	3-4			
Dorsal		7	5	11
Ventral		7	7	10
Degree of stripe continuity:				
Anterior bar:				
Dorsal	5-13	Separate	Separate	Continuous
Ventral		Continuous	Separate	Continuous
Posterior bar:				
Dorsal	13-16	Separate	Continuous	Continuous
Ventral		Continuous	Separate	Continuous
Head melanophores	4-8	—	—	More on dorsal surface and snout
Melanophores on ventral surface of gut	>13	1-2 rows of spots	No spots or a few reduced spots	1-2 rows of spots
Lateral pigment on gut surface	<13	—	Much less	—
Mediolateral pigment in postanal region	5-8	—	—	More
Ventral caudal pigment	<10	Row of spots	Isolated spots	Isolated spots
Number of rays on superior hypural element	>13	5	4	4

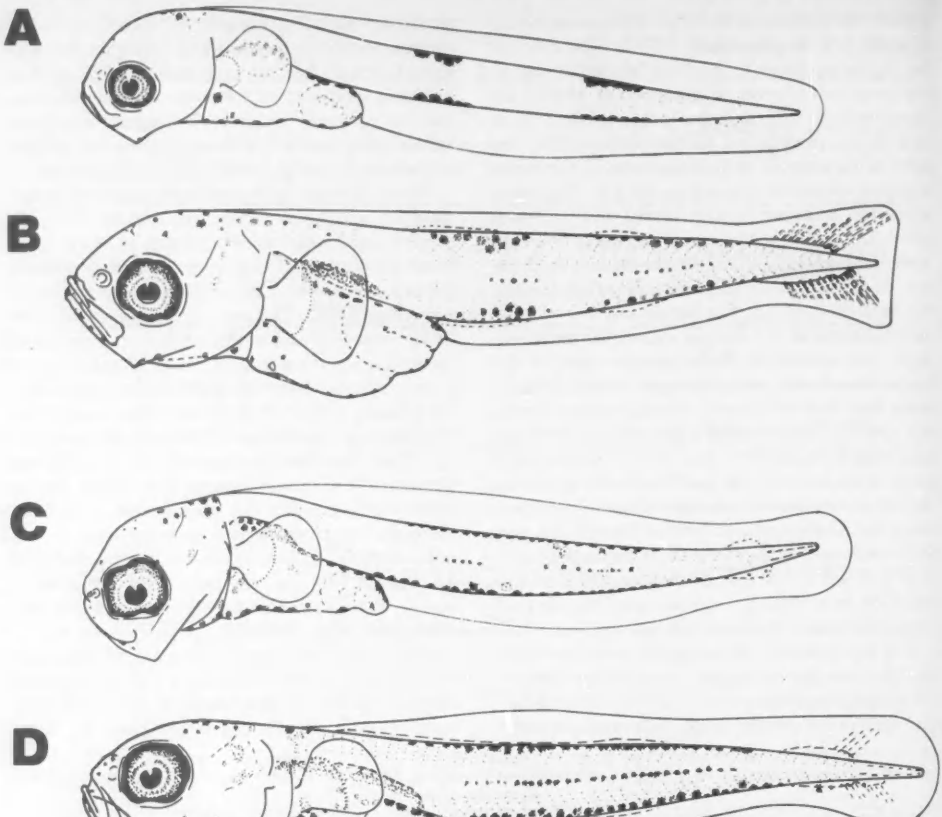


FIGURE 5.—Larvae of *Theragra chalcogramma* and *Gadus macrocephalus*: A. *T. chalcogramma*, 6.2 mm SL; B. *T. chalcogramma*, 9.8 mm SL; C. *G. macrocephalus*, 5.6 mm SL; D. *G. macrocephalus*, 8.5 mm SL.

rocephalus. This character can be useful in a size range (>13.0 mm SL) which may be troublesome when pigment patterns are no longer helpful and adult characters (e.g., barbel length, mouth and anus position, or shape of fins) are not fully developed. Larvae >20.0 mm SL may also be distinguished by a combination of meristic counts (Table 1).

ACKNOWLEDGMENTS

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NOTES

PREDATION BY SHARKS ON PINNIPEDS AT THE FARALLON ISLANDS[1]

What we know about mortality in pinnipeds has largely been derived indirectly. For example, pinnipeds or parts thereof have occasionally been found in shark stomachs. Sharks have thus become known as pinniped predators (e.g., Gogan[2]), but, since few direct observations of shark/pinniped interactions exist, we do not know the extent of such predation. The present paper summarizes observations of shark/pinniped encounters at the Farallon Islands between 1970 and 1979. We relate the frequency of observed encounters to annual and seasonal changes in pinniped population, and the marine climate, and assess the effect of shark-bite injury on the reproductive performance of seals.

Methods

The South Farallon Islands, San Francisco County, Calif. (lat. 37.4° N, long. 123.0° W), lie at the inward edge of the California Current, 30 km west of the California coast. Southeast Farallon, West End, and accompanying rocks compose the South Farallones and in all are about 44 ha (Figure 1). Over 250,000 seabirds of 12 species breed there (Ainley and Lewis 1974). Pinnipeds reach a peak of 2,500 animals—three species breed and occur there year-round: harbor seal, *Phoca vitulina*, northern elephant seal, *Mirounga angustirostris*, and northern sea lion, *Eumetopias jubatus*; a fourth, California sea lion, *Zalophus californianus*, the most numerous of Farallon pinnipeds, occurs most abundantly in spring, but few breed there; and a fifth, northern fur seal, *Callorhinus ursinus*, occasionally hauls out (Pierotti et al. 1977; Ainley et al.[3]).

Since 1968, the Point Reyes Bird Observatory has maintained a year-round research station on Southeast Farallon. On a rotating but continual schedule at least two biologists, plus several volunteer workers, have operated the station. Every day, weather permitting, a census of birds and a general visual survey of inshore waters was made. Beginning in 1970 elephant seals were

[1]Contribution 169 of the Point Reyes Bird Observatory.

[2]Gogan, P. J. P. 1977. A review of the population ecology of the northern elephant seal, *Mirounga angustirostris*. Unpub. manuscr., 68 p. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sandpoint Way, NE., Seattle, WA 98115.

[3]Ainley, D. G., H. R. Huber, R. P. Henderson, T. J. Lewis, and S. H. Morrell. 1976. Studies of marine mammals at the Farallon Islands, California, 1975-76. Final report, Marine Mammal Commission (Contract No. MM5AC027), Wash., D.C., available Natl. Tech. Inf. Serv., Springfield, VA 22151 as PB 2-266249, 32 p.

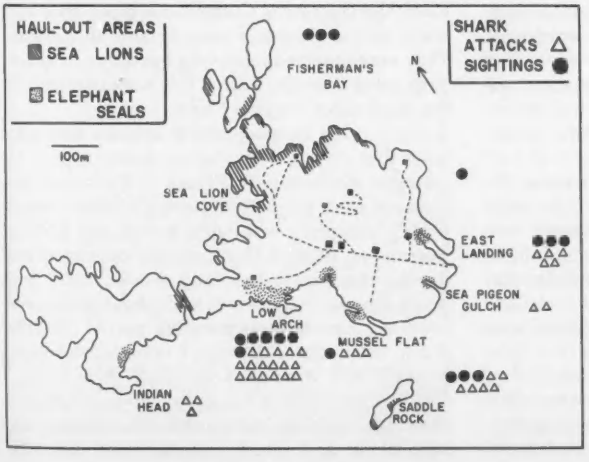

FIGURE 1.—South Farallon Islands, central California, and location of observed shark/pinniped encounters and major haul-out areas of sea lions and elephant seals.

censused weekly during most of the year and daily during the breeding season. Regular weekly censuses of other pinnipeds have been conducted since 1972, and as far back as 1970 irregular counts were made. Since we found shark activity to be seasonal (see below), we included comments on the seasonal changes in sea-surface temperature and salinity. Such information was derived from daily readings made at noon (P.s.t.).

Results

We recorded events involving sharks 58 times between 9 September 1970 and 9 February 1979. Of these, 37 were definite observations of sharks eating pinnipeds (i.e., "shark attacks") and the remainder (21) were mostly of sharks seen within 1 km of the island. In definite shark attacks, we were first (36 of 37 times) alerted to the incident by a flock of gulls (mostly the western gull, *Larus occidentalis*), hovering above a large bloody area (5 m^2) in the water. Usually we saw the shark's head and dorsal and caudal fins which offered clues to species identification and estimation of size and number. We often saw the pinniped prey as well. On five occasions only an area of bloody water and the hovering gulls were observed. These, too, were likely shark attacks on pinnipeds, but we did not include them in the 37 known attacks. Observations, from discovery of the gull flock to dissipation of blood and gulls, lasted from 3 to 15 min. If the carcass was not consumed in that time, then its disappearance was probably due to sinking. In the areas of most shark/pinniped interactions the water was 4-12 m deep.

In 20 interactions we saw the pinniped prey sufficiently well for a positive identification. Two involved sea lions, one or perhaps two involved harbor seals, and the remainder involved elephant seals. Based on size, we could tell that seven elephant seals were young individuals, about 3 yr old or less, and an eighth was an adult female. On rare occasions, we have observed sea lions with obvious, fresh shark-bite wounds. However, the location of most shark attacks in the vicinity of the elephant seal hauling out areas (Figure 1) further supports what other data indicate, that at Southeast Farallon, sharks more frequently ate elephant seals than other pinnipeds.

In 30 instances, the white shark, *Carcharodon carcharias*, was identified as the species seen preying on seals. All were at least 3 m long and most about 3.5-5 m long. In 16 of 21 nonattack observations within 1 km of the island, the shark was also identified: 14 involved white sharks and two involved the blue shark, *Prionace glauca*. How many sharks were present at any one time is not known. On at least three occasions two sharks, and once three sharks, simultaneously fed on one pinniped. On 8 January 1976, a 3 m long white shark was caught in Fisherman's Bay and 7 d later two larger white sharks were seen on the opposite side of the islands.

Sharks were more abundant or more active during the late fall and winter over the 9 yr (Figure 2). The number of attacks in December and January was perhaps artifically low (see below) because on many days during those months few if any gulls were present to alert observers. The possibility that attacks were missed was particularly likely in December 1976 and January 1977. Sharks were known to be present then because several seals hauled out with fresh shark-bite wounds and part of another was seen floating in the water. Yet no attacks were seen. The timing of greatest shark activity corresponded closely with the Davidson Current period (October-February) which, as described by Bolin and Abbott (1963), is characterized by slowly declining sea-surface temperatures and salinities and the appearance of a northward flowing countercurrent (shoreward of the south-flowing California Current). White sharks were thus present (or at least active, see below) when waters were warm but not necessarily the warmest (Figure 2). Blue sharks, on the other hand, were definitely most abundant during the warm oceanic period (July-September), when the California Current slackens, allowing warm saline oceanic waters to flow shoreward. They were observed commonly but only at 3 km or more away from the island. Few were involved in the observations reported here.

The timing of most shark attacks also corresponded closely with the late autumn peak in elephant seal numbers (Figure 2). Each year the elephant seals reached maximum numbers twice, during midspring and again during late fall (Le Boeuf et al. 1974). A third, smaller peak occurred during the winter breeding season. Only two shark attacks, both involving elephant seals, were observed during the upwelling period (March-July), when the California Current flows most strongly and temperatures reach their lowest. One of these attacks occurred during the spring peak in elephant seal numbers. During the fall, when most shark attacks were observed,

the populations of other pinniped species at the Farallones were usually near their annual low (Ainley et al. footnote 3), which indicates even further that elephant seals were the usual prey of sharks. Rather exceptional were the high numbers of California sea lions present in the fall 1978 (Huber et al.[4]). Sharks and shark incidents were seen often then but we could identify few of the pinniped prey. One incident definitely involved a sea lion but most others occurred in areas frequented by elephant seals and not by sea lions.

Several elephant seals arrived at the Farallones for the breeding season bearing shark-bite wounds, some fresh and some healed. The histories of these animals are noteworthy, particularly since their being severely wounded may have affected their reproductive performance. Twenty-four breeding attempts by females identifiable as individuals were available for analysis. In 10 attempts, females arrived with fresh wounds. In only one (10%) did she successfully rear a pup by herself, three lost their pups, three received help from other cows (i.e., they shared suckling), and three apparently did not pup. In 1977 three newly wounded cows disappeared (not even present during spring molt) after leaving the island with healed wounds. In 14 pupping attempts by known females with no wounds (but wounded in a later year) or with old, healed wounds, all but two (86%) successfully raised a pup without help. The difference is significantly different from the 10 attempts mentioned above ($t = 3.3$, $P<0.001$). Since many of the freshly wounded females were probably pupping for their first time, it could have been lack of experience that resulted in their poor record rather than being wounded. Two females, however, without wounds raised their first pups successfully but the next season, each with a fresh wound, they either allowed another cow to help in suckling or failed to pup successfully. In addition, of 11 females pupping for their first time in 1977 and not having shark-bite wounds, 7 (64%) were successful, and only 1 allowed its pup to be nursed by another female. Thus females with fresh, severe shark-bite wounds were less successful in pupping than others. Perhaps the energy and tissue-building resources needed to heal a severe wound were taken from those required in the rearing of a pup. None of the 6 females with fresh shark wounds in the 1977 breeding season was observed to copulate; among other females 99 (77%) were observed in copulation.

Two male elephant seals have also hauled out at the Farallones, bearing shark-bite wounds. One first visited in December 1972 as a subadult bull (probably about 5 yr old) and had an old shark-bite wound. He returned each season through the 1976 breeding season. Another was first seen in 1972 as a young adult (Le Boeuf et al. 1974) and was the alpha bull in the breeding hierarchy during 1972, 1973, and 1974. In 1975 he arrived for the fourth year, was initially the alpha bull, but was dethroned before the end of the breeding season. In 1976 he appeared on the island with two fresh shark wounds. Thereafter he visited the breeding colony intermittently, but was not part of the hierarchy of breeding bulls.

[4]Huber, H. R., D. G. Ainley, S. H. Morrell, R. R. LeValley and C. S. Strong. 1978. Studies of marine mammals at the Farallon Islands, California, 1977-78. Final report, Marine Mammal Commission (Contract No. MM7AC025), Wash., D.C., available Natl. Tech. Inf. Serv., Springfield, VA 22151 as PB 80-111602, 50 p.

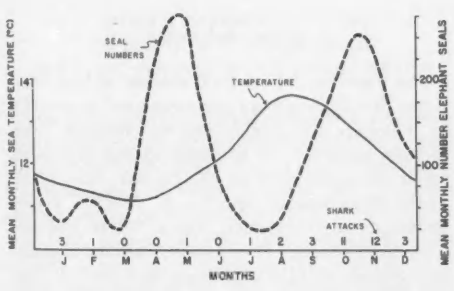

FIGURE 2.—Annual cycles in monthly mean sea-surface temperature, elephant seal numbers and number of shark/pinniped interactions in the Farallon Islands, central California, vicinity, 1970-78. Seal numbers are from Ainley et al. (text footnote 3) and Huber et al. (text footnote 4).

Discussion

It is obvious that the frequency of shark attacks on pinnipeds and other shark observations have been increasing at the South Farallon Islands (Table 1). We are convinced this is not an artifact of increasing observer awareness for a number of reasons, because a flock of 50+ gulls hovering for 10-15 min above a large, blood-red patch of water within 50 m of shore is not easy to miss, particularly from such a small island; and daily censuses have been conducted consistently since 1970.

Since the seasonal occurrence of some sharks is related to water temperatures (e.g., O'Gower

TABLE 1.—Annual data on elephant seal numbers, shark attacks, water temperatures, and frequency of attacks relative to seal numbers at the Farallon Islands, central California.

	Winter (late December-February)				Summer (late March-early July)				Fall (late August-mid-December)			
Year	A Max no. seals	B No. attacks	C Ratio A:B	Mean sea temp	A Max no. seals	B No. attacks	C Ratio A:B	Mean sea temp	A Max no. seals	B No. attacks	C Ratio A:B	Mean sea temp
1970	0	0	0	11.3	60	0	0	10.0	35	[1]1	0	15.5
1971	0	0	0	11.5	50	0	0	[2]8.8	120	0	0	16.8
1972	3	0	0	11.5	120	0	0	10.0	155	1	.01	17.0
1973	10	0	0	12.1	176	0	0	10.8	170	2	.01	14.5
1974	20	0	0	11.0	290	1	.003	8.8	300	2	.01	15.0
1975	30	[2]0	0	10.9	305	0	0	10.0	330	6	.02	13.5
1976	55	0	0	10.5	460	0	0	9.3	450	4	.01	16.0
1977	110	[2]0	0	12.7	523	0	0	10.0	507	7	.01	13.8
1978	182	4	.02	13.6	717	1	.001	12.4	609	7	.01	12.0
1979	250	[2]1	.004	11.6	776	0	0	11.2				

[1] Thought to be an attack on a sea lion.
[2] Cows arrived with fresh shark-bite wounds; in 1979 the remains of a cow, likely a shark victim, was seen floating in the water.

and Nash 1978), it was worthwhile to consider the relationship between temperature and sharks at the Farallones. As shown in Table 1, water temperature during the fall when most shark attacks and sightings occurred, compared among the years, fluctuated up and down but did not relate clearly to yearly fluctuation in shark attack frequency. The same was true for temperatures during the winter elephant seal breeding season. The year 1978 provides an instructive example of this. In the spring-summer, temperatures were unusually high. In spite of record numbers of elephant seals only one shark attack was observed, and that occurred in July, long after the seal population peak (only 24 were present; 452 sea lions, though, were present). Later in the fall, temperatures were lower than during spring but much shark activity was evident (Table 1). The only major relationship that was evident between shark attacks and water temperature was that all but one observed attack occurred when temperature generally exceeded 12° C (as summarized in Figure 2). Unfortunately, there is no published information of the seasonality of white sharks to explain this. Off Durban, South Africa, where water temperatures are higher than at the Farallones, Bass (1978) found small white sharks more abundant when temperatures dropped to the annual low (equivalent to highest Farallon temperatures), but the number of white sharks the size of those at the Farallones did not change.

The factor that best relates to the general increase in white sharks is an increase in elephant seal numbers. The fall, winter, and spring populations of elephant seals have been increasingly rapidly at the Farallones over the past several years (see Le Boeuf et al. 1974; Ainley et al. footnote 3; Table 1). The seal population during the fall, the period of most shark attacks, has increased about 3.9 fold since 1972, the first year of the period when shark attacks have been seen consistently year after year. In the fall data there is a direct relationship between the number of shark attacks and the number of seals ($r = 0.895$; $P<0.01$). The ratio of attacks to the number of seals, except during spring and the 1979 seal breeding season, has remained at about 0.01-0.02.

Shark attacks during the elephant seal breeding season (winter) have been observed less often than during the fall but they may be increasing during that period, too, if the 1977-79 seasons are any indication. Interestingly, attacks were first seen during winter in the year when the elephant seal population surpassed 120 animals (1978), the same population level that occurred in conjunction with the first fall sighting of elephant seal/shark interactions (1972). This further indicates a density-dependent relationship between shark predation and elephant seal populations.

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Follett kindly reviewed some photographs that we took of sharks, thus confirming our identifications, and checked an earlier version of this paper.

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IN SITU OBSERVATIONS ON REPRODUCTIVE BEHAVIOR OF THE LONG-FINNED SQUID, *LOLIGO PEALEI*

There are several published accounts of reproductive behavior, including copulation and egg laying, of the long-finned squid, *Loligo pealei* Lesueur, in the laboratory (Drew 1911; Arnold 1962); but with the exception of Stevenson's (1934) field observations of *L. pealei*'s behavior around an egg mass, no in situ observations of egg-laying behavior have been documented for this species. Field and laboratory observations of reproductive behavior have been made for the California market squid, *L. opalescens* (McGowan 1954; Fields 1965; Hobson 1965; Hurley 1977), the tropical arrow squid, *L. plei* (Waller and Wicklund 1968), *L. bleekeri* (Hamabe and Shimizu 1957), *L. vulgaris* (Tardent 1962), the broad squid, *Sepioteuthis bilineata* (Larcombe and Russell 1971, and *S. sepioidea* (Arnold 1965). However, each species' in situ egg-laying behavior differed from the behavior we observed in *L. pealei*.

Observations

Each summer *L. pealei* and its egg masses are common in shallow coves along the coast of Rhode Island, such as our study site at Fort Wetherill on Conanicut Island in Narragansett Bay. Scuba divers, including ourselves, have observed squid to be numerous in these areas, particularly at night when they occur singly or in small, loosely formed schools.

On 16 June 1979, at 1230 h on an incoming tide (temperature 14.5°-15.0° C, depth 6 m) using scuba we observed a large squid egg mass (50-60 cm across) attached to one side of a small boulder. The surrounding area was a sandy/mud bottom with unattached fragments of the seaweeds *Ulva lactuca*, *Laminaria* sp., and *Porphyra* sp. Because the egg mass was larger than the 12-15 cm masses we regularly see in this area while diving, we spent some time observing it. Squid began to appear at the limit of the water visibility (about 4.0 m) and moved toward the egg mass in a semicircle. They stopped about 2.5-3.0 m from the mass and remained stationary approximately 1-m off the bottom. The squid were in well-defined pairs with the smaller females (mantle length 16-18 cm) parallel to and on the left of each male (20-22 cm) as we faced them (Figure 1). Eight pairs were visible at that time. The animals had moderate pigmentation over the mantles, but we did not observe the distinctive spots of color at the base of the arms as were reported by Arnold (1962), nor did we observe color changes during the observation period. Contrary to McGowan's (1954) observations on *L. opalescens*, all of the animals appeared to be in good condition; no torn epithelium was obvious and no dead or dying individuals had been seen in the area of the egg mass or anywhere else in the cove during the hour-long dive.

One pair of squid at a time approached the egg mass with their arms held forward and tentacles extended. Because of our position directly facing the squid, it was impossible to observe the beginnings of an egg finger protruding from the funnel as Drew (1911) and Tardent (1962) had observed in

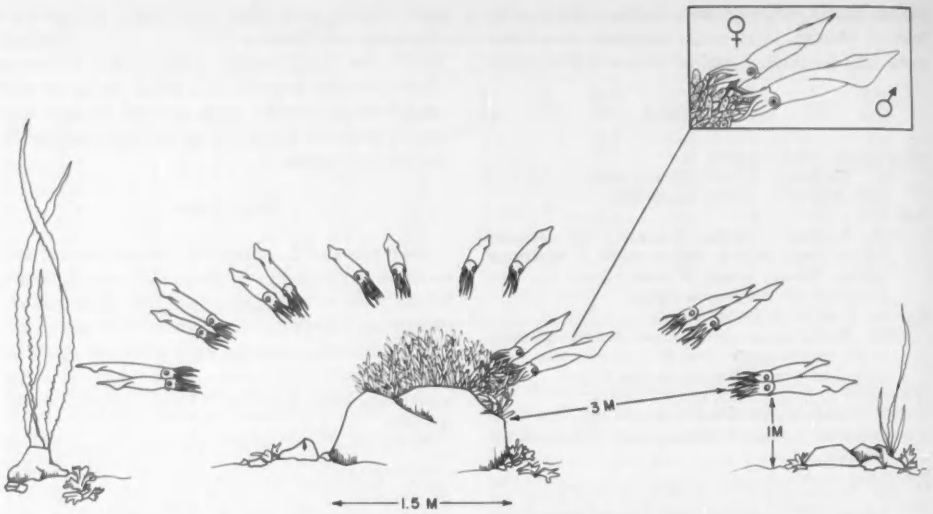

FIGURE 1.—Pairs of squid formed a semicircle and one pair at a time approached the egg mass. The female and male intertwined arms as they extended them into the egg mass. We surmise that the female was depositing an egg capsule and that the male was exhibiting parental care or "grooming" behavior. Water depth was 6 m.

L. pealei and *L. vulgaris* held in aquaria. However, comparing the behavior of the animals with that described in literature on squids' reproductive behavior, we concluded that the females were depositing egg capsules. They intertwined arms as they extended them into the egg mass. The arms of the male appeared to move delicately over and among the existing fingers of eggs (Figure 1). Each pair that approached the egg mass stayed 2-4 s then moved backward into the same position it had previously occupied in the semicircle. At that time another pair moved forward. There did not appear to be any order in which pairs approached the egg mass; however, no more than one pair approached at any given time. The same pair approached more than once.

Although most accounts indicate that copulation occurs just before egg deposition, our observations cannot substantiate this because egg laying had already commenced. No agonistic behavior which is often associated with reproduction was evident during the 10-min observation period.

Discussion

The social hierarchy involving egg deposition differs from species to species. Observations of *L. opalescens* and *L. plei* in the field indicate that once copulation occurs, individual pairs break apart and the female approaches the egg mass and deposits a capsule alone, although Hurley (1977) did observe an *L. opalescens* male pushing a female toward an egg mass. *Sepioteuthis sepioidea* remains paired after copulation, but only the female approaches the egg mass during egg laying (Arnold 1965). Larcombe and Russell (1971) reported that *S. bilineata* also remains paired, but the male escorts the female to the egg mass. However, the male assumes a protective role and follows about 0.5 m behind and above the female so he is between her and the other squid during the 2 s period in which she deposits a capsule. In contrast, *L. pealei* pairs formed and maintained a semicircle throughout egg laying (Figure 1). One pair at a time approached the egg mass; the male did not appear to assume a protective role, but might have been involved in "grooming" such as Tardent (1962) described for *L. vulgaris* held in an aquarium. Parental care or guarding egg masses has been documented for *L. pealei* by Stevenson (1934), who noted that both solitary males and pairs patrolled and guarded an egg mass. Similar guarding behavior has also been reported for *L. opalescens* (Hurley 1977).

Although there are similarities in reproductive behavior among several squid species, our observations of *L. pealei* indicate a social structure which is well defined and different from that described for other species with the possible exception of *S. bilineata* and *S. sepioidea*. Since there are relatively few published accounts of in situ copulation and egg-laying activities, it is difficult to know what is normal and what might be altered behavior patterns due to the presence of human observers, submersibles, lights, etc. However, our observations and those of other divers, including two in the same area a week earlier who reported 12-15 pairs of squids in a semicircle (Turco[1]), indicate that the social structure associated with egg-laying behavior is not an isolated phenomenon, but a pattern which is recurrent in populations of *L. pealei* which frequent New England coastal waters in the summer.

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SPAWNING AND SEXUAL MATURITY OF GULF MENHADEN, *BREVOORTIA PATRONUS*[1]

Earlier studies of egg and larva collections (Turner 1969; Fore 1970; Christmas and Waller[2]) have shown that Gulf menhaden, *Brevoortia patronus*, which range throughout the northern Gulf of Mexico from Cape Sable, Fla., to Veracruz, Mexico, spawn from about October to March from near shore to about 97 km offshore at depths of from 2 to 111 m. There have been two previous studies to determine the age of spawning, the number of ova produced, and the peak time of ovary maturation (Suttkus and Sundararaj 1961; Combs 1969). Our objectives in the present study were to: 1) estimate the minimum number of maturing ova for specific age-groups and size groups, 2) estimate the percentage of fish that spawn at each age, 3) determine the time of spawning, and 4) determine the frequency of spawning.

Gulf menhaden make annual inshore-offshore movements. The larvae spend 3-5 wk in offshore waters before moving into estuaries where they

[1]Southeast Fisheries Center Contribution No. 81-12B.
[2]Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr., 20 p. Gulf Coast Res. Lab., Ocean Springs, Miss. (NMFS contract no. 03-4-042-24).

transform into the adult form (Reintjes 1970). The following autumn the juveniles, ranging in fork length from about 55 to 130 mm FL, migrate from the estuaries to offshore waters (Tagatz and Wilkens 1973), along with all other age-groups that are moving from inshore waters of the gulf at this time. Fish of all age-groups migrate to inshore waters again the following spring.

While in inshore waters, age 1 and older Gulf menhaden are subject to an intensive purse seine fishery that extends from Florida to eastern Texas from about mid-April to early October. The fish are processed into meal, oil, and solubles at plants in Mississippi and Louisiana.

During the purse seine season Gulf menhaden are sexually inactive. Therefore, gonads collected at that time are of no use for fecundity studies. The only source of Gulf menhaden during the spawning season is the offshore groundfish trawl fishery, which takes Gulf menhaden incidentally along with the primary species. Catches are landed at plants in Mississippi and Louisiana and processed as canned pet food (Roithmayr 1965). The number of Gulf menhaden taken varies, but is never large. From October 1976 to February 1977, 241 females (124-257 mm FL) and 516 males (113-240 mm FL) were collected from the groundfish landings. After January, we were able to collect only 4 maturing females in February and none in March or April.

To assure that Atlantic menhaden, *B. tyrannus*, were assigned to the correct year class, June and Reintjes (1959) developed specific criteria for assigning fish to year classes on the basis of annulus formation. These criteria also were adopted when the investigation of Gulf menhaden was begun in 1964. March 1 was designated as an arbitrary date on which all fish of a given year class were advanced 1 yr in age, regardless of whether or not a new annulus had formed. Since all fish used in this study were collected from October to February, an age-1 fish is one that has one annulus, but has completed two growing seasons; an age-2 fish has two annuli but has completed three growing seasons.

All fish were caught in the northern Gulf of Mexico from lat. 28°35′ to 30°15′ N and from long. 87°45′ to 91°28′ W. Fork lengths were measured to the nearest millimeter and wet weights to the nearest 0.1 g. Scale samples for aging were taken from the left side of the body along the midline and below the origin of the dorsal fin. Paired gonads were preserved in a 10% buffered Formalin[3] solution.

Stages of Sexual Maturity

Preserved gonads were blotted to remove excess moisture and weighed to the nearest 0.01 g. A sample of 0.1 g or less was cut from the central portion of an ovary and examined microscopically to describe morphology of developing ova and to determine the mean diameter of the largest ova present.

Four groups of ova were found in the most advanced ovaries, while only one to three groups were found in less developed ovaries. Immature ova were under 0.20 mm in diameter, translucent, and contained an irregular spherical nucleus. Intermediate ova ranged from 0.20 to 0.35 mm and had a dark or opaque center surrounded by a wide sphere of dull yellowish to brownish speckling. Maturing ova were 0.36 to 0.72 mm, opaque, and had an outer translucent covering or tissue. Ripe ova were similar to maturing ova except they were >0.72 mm.

Three stages of sexual maturity were recognized on the basis of the most advanced group of ova present: immature, intermediate, and maturing. Fish classified as maturing contained either maturing or both maturing and ripe ova. All maturing or ripe ova in a sample were counted and about 100 were selected randomly and measured for diameter.

Age and Size of First Spawning

Gulf menhaden <135 mm can be considered as age-0 fish (Nicholson and Schaaf 1978). All fish <100 mm FL that we examined showed no evidence of maturing ova. Through December, 63% of age-1 fish and 71% of all fish age 2 or older in our samples contained maturing ova. By January all fish age 1 or older contained maturing ova (Table

[3]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of female Gulf menhaden sampled from October 1976 to February 1977 by age, month, and stage of sexual maturity (immature or mature).

Month	Age 1		Age 2		Age 3		Age 4
	Immature[1]	Mature	Immature	Mature	Immature	Mature	Mature
Oct.	5	6	3	10			
Nov.	4	15		3			
Dec.	4	1	4	3	1	3	1
Jan.		19		3		2	
Feb.		3		1			

[1]Fish with intermediate ova (as the largest ova present) were included in this category.

TABLE 2.—Number of female Gulf menhaden sampled from October 1976 to February 1977 by fork length, month, and stage of sexual maturity (immature or mature).

Fork length (mm)	Oct.		Nov.		Dec.		Jan.	Feb.
	Immature[1]	Mature	Immature	Mature	Immature	Mature	Mature	Mature
120-129	2							
130-139	1							
140-149			1	1				
150-159			2	3	1		1	
160-169	5	1	2	8	1		6	1
170-179	7	15	2	15	1	2	10	2
180-189	6	17		15			2	
190-199	5	20		12	2		2	
200-209	3	14		11	3	1	3	1
210-219	1	3		1		4	1	
220-229		3		1	1	2	2	
230-239		1		4		1	5	
240-249				1		1	1	
250-259							1	

[1]Fish with intermediate ova (as the largest ova present) were included in this category.

1). For both aged and unaged fish >140 mm that we examined, 73% contained maturing ova in October, 91% in November, 55% in December, and 100% in January and February (Table 2). From this information we concluded that Gulf menhaden spawn for the first time at age 1, after they have completed two seasons of growth, and then continue to spawn each year thereafter.

Time and Frequency of Spawning

Previous studies of egg and larva collections (Turner 1969; Fore 1970; Christmas and Waller footnote 2) and of increases in gonad weights (Suttkus and Sundararaj 1961; Combs 1969) have indicated that spawning begins in October and ends about March. Our data also show that spawning occurs within this time period. For each month we plotted the mean gonad weight as a percentage of body weight for those fish we were able to age (Figure 1). For females the means, which were already high in October, indicating that gonadal development had begun, increased in November and December and then decreased in January and February. Generally, males followed the same pattern as females when both aged and unaged were combined (Figure 2). We can not explain why the relative gonad weights of age-1 females were higher than those of older fish, unless some of the older fish had partially spawned by the time they were collected, thereby decreasing their gonad weight.

The number of times an individual fish will spawn during a season may be inferred from the difference in size between groups of ova. If there is

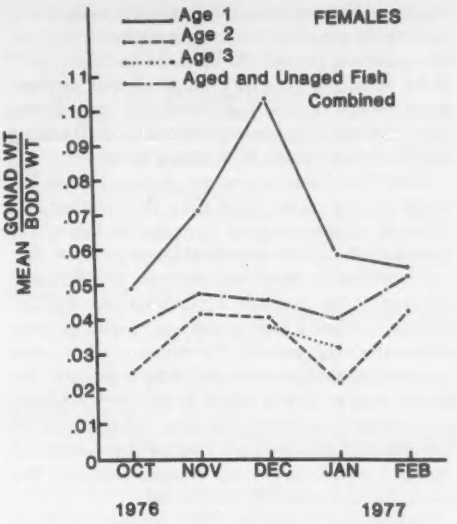

FIGURE 1.—Relation between mean of gonad weight/body weight and month for unaged and different age-groups of female Gulf menhaden.

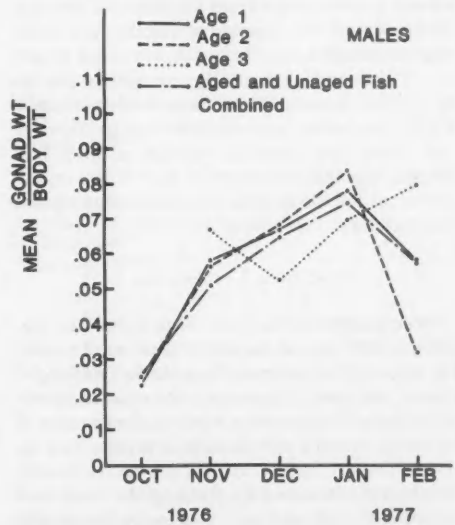

FIGURE 2.—Relation between mean of gonad weight/body weight and month for unaged and different age-groups of male Gulf menhaden.

a large difference in size between immature ova, developing intermediate ova, and maturing ova, the spawning period will be short and definite. If there is only a gradual change in size between these groups of ova, individual fish may spawn several times over an extended period (Hickling and Rutenberg 1936; de Vlaming 1974).

Since there was a gradual change in size between groups of ova, and since the number and diameter of maturing or ripe ova for fish of the same length varied considerably, we inferred that Gulf menhaden were intermittent, or fractional spawners. The number of maturing ova did not change markedly from month to month, or even within the same month. The ripe ova, after being spawned, probably are replaced by a group of the largest maturing ova which in turn are replaced by a group of intermediate ova. Perhaps four or five different groups of ova ripen and are spawned during a single spawning season, although the exact number cannot be estimated.

Higham and Nicholson (1964) stated that, from available evidence, it is impossible to decide conclusively the frequency of spawning of individual Atlantic menhaden but they favored the hypothesis of maturation and fractional spawning of more than one group of ova during the season.

Combs (1969) concluded that *B. patronus* spawns several times from October to February. He found that over a period of months spawnable oocytes occurred together with advanced stages of ova that were potentially spawnable. He described the histological events in the development of Gulf menhaden ova from formation to maturity and found that once the provisional yolk had formed, ova lost all potential to remain in the ovary and had to complete their development prior to spawning or be aborted.

Number of Ova Spawned

Since analysis of variance tests showed no significant difference in the size or number of maturing ova in gram samples from the left and right ovaries, we used either ovary for measurements and counts. (Counts were made of the number of maturing ova in a sample of 0.1 g or less from an ovary.) The number of maturing or ripe ova in each female was estimated by dividing the combined weight of the left and right ovaries by the sample weight and multiplying this number by the number of maturing or ripe ova in the sample.

If fractional spawning occurs, the number of ova estimated to have been spawned by fish of any given age or size would necessarily be minimal, since some ova probably would have been spawned by the time some ovaries were collected. Fractional spawning also would increase the variability in the number of ova estimated for fish of the same age or size (Bagenal and Braum 1971). Of the 70 maturing females that we could age, 44 were age 1, 20 were age 2, 5 were age 3, and 1 was age 4. The mean number of ova and its standard error for each age-group respectively were 37,100±3,467; 47,900±5,038; 61,800±9,486, and 151,000.

Three relationships that are most useful in explaining and understanding population dynamics of a species are those of fecundity with age, length, and weight. To determine what mathematical models would be most appropriate in describing these relations, we used Statistical Analysis System[4] to test various statistical regression models. We chose those which had the greater r^2 values and the minimum deviations from the regression line. In the following models F = fecundity, A = age, L = fork length, and W = body weight. For fecundity on age (Figure 3):

[4]Statistical Analysis System; Barr, Goodnight, Sall and Helwig, SAS Institute Inc., P.O. Box 10066, Raleigh, NC 27506.

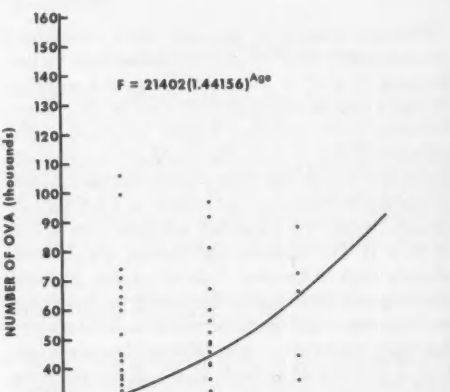

FIGURE 3.—Relation between number of maturing ova and age for Gulf menhaden.

$$\log_e F = 9.9713 + 0.3657(A)$$
$$(r^2 = 0.1804,\ s_{y \cdot x} = 0.5466).$$

For fecundity on fork length (Figure 4):

$$\log_e F = -9.8719 + 3.8775(\log_e L)$$
$$(r^2 = 0.6490,\ s_{y \cdot x} = 0.3751).$$

For fecundity on weight:

$$F = 12{,}064.2908 + 374.8848(W)$$
$$(r^2 = 0.4445,\ s_{y \cdot x} = 20{,}427.0752).$$

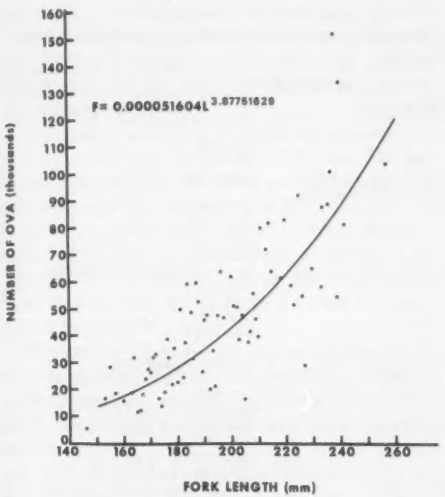

FIGURE 4.—Relation between mean number of maturing ova and fork length for Gulf menhaden.

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FOOD OF THE PACIFIC WHITE-SIDED DOLPHIN, *LAGENORHYNCHUS OBLIQUIDENS*, DALL'S PORPOISE, *PHOCOENOIDES DALLI*, AND NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, OFF CALIFORNIA AND WASHINGTON

Our knowledge of the feeding habits of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, and the Dall's porpoise, *Phocoenoides*

dalli, is based on examination of the stomach contents of stranded animals, animals accidentally taken in commercial fishing gear, those taken in the western Pacific commercial fishery, and animals that died during capture attempts. Of these only a few were normally feeding animals taken at sea, whose stomach contents were thoroughly examined. Fishes and squids previously identified from stomachs of dolphins and porpoises by various investigators are listed in Table 1.

This paper documents the stomach contents of 44 Pacific white-sided dolphin and 9 Dall's porpoise collected at sea off California and Washington. All animals were collected by the authors during pelagic fur seal studies with the exception of three dolphins which were collected by a staff biologist during whale research voyages off California. Comparisons of stomach contents are made between the Pacific white-sided dolphin, Dall's porpoise, and northern fur seal, *Callorhinus ursinus*, collected near the same locations and usually on the same day. Mention of the dolphin, porpoise, and seal in this paper refers to the above-named species only unless noted otherwise.

The Pacific white-sided dolphin ranges the eastern North Pacific Ocean, from Baja California

TABLE 1.—List of fishes and squids previously identified in stomachs of Pacific white-sided dolphin and Dall's porpoise from the North Pacific Ocean by localities.

Locality and species	Reference source	
	Pacific white-sided dolphin	Dall's porpoise
California:		
Pacific herring, *Clupea harengus pallasi*		Loeb 1972
Pacific sardine, *Sardinops sagax*	Higgins 1919	
Northern anchovy, *Engraulis mordax*	Brown and Norris 1956; Norris and Prescott 1961; Fiscus and Niggol 1965; Fitch and Brownell 1968	Loeb 1972
Night smelt, *Spirinchus starksi*		Loeb 1972
California smoothtongue, *Bathylagus stilbius*		Loeb 1972
Pinpoint lampfish, *Lampanyctus regalis*		Loeb 1972
Blue lanternfish, *Tarletonbeania crenularis*		Loeb 1972
Pacific whiting, *Merluccius productus*	Best 1963; Fiscus and Niggol 1965; Fitch and Brownell 1968	Norris and Prescott 1961; Best 1963; Loeb 1972
Cusk-eel, *Otophidium taylori*		Loeb 1972
Eelpouts, Zoarcidae		Loeb 1972
Grenadier, Macrouridae		Loeb 1972
Pacific saury, *Cololabis saira*	Houck 1961	
Jack mackerel, *Trachurus symmetricus*	Scheffer 1953; Norris and Prescott 1961; Houck 1961	Norris and Prescott 1961
Pacific pompano, *Peprilus simillimus*		Loeb 1972
Rockfish, *Sebastes* spp., juvenile		Loeb 1972
Sablefish, *Anoplopoma fimbria*, juvenile		Loeb 1972
Snailfish, *Liparis* sp.		Loeb 1972
Pacific sanddab, *Citharichthys sordidus*		Loeb 1972
Eels, Anguilliformes		Loeb 1972
Squid, *Loligo opalescens*	Brown and Norris 1950; Ridgway 1966	Norris and Prescott 1961; Loeb 1972
Squid, *Abraliopsis* sp.		Loeb 1972
Squid, *Gonatus* sp.	Fiscus and Niggol 1965	Loeb 1972
Squid, *Onychoteuthis borealijaponicus*		Loeb 1972
Octopus, *Octopus bimaculatus*		Loeb 1972
British Columbia:		
Pacific herring, *Clupea harengus pallasi*		Cowan 1944
Gulf of Alaska:		
Capelin, *Mallotus villosus*		Scheffer 1953
Japan:		
Anchovy, *Engraulis japonica*	Hotta et al. 1969	
Sudidae, *Paralepis* sp.		Wilke and Nicholson 1958
Lanternfish, Myctophidae—Scopelidae	Wilke et al. 1953	Wilke et al. 1953
Lanternfish, *Notoscopelus* sp.		Wilke and Nicholson 1958
Lanternfish, *Diaphus* sp.		Wilke and Nicholson 1958
Lanternfish, *Tarletonbeania taylori*		Wilke and Nicholson 1958
Lanternfish, *Lampanyctus* sp.		Wilke and Nicholson 1958
Lanternfish, *Myctophum* sp.		Wilke and Nicholson 1958
Cod, *Laemonema longipes*		Wilke and Nicholson 1958
Hake, *Laemonema morsum*		Wilke et al. 1953
Mackerel, *Scomber japonicus*	Wilke et al. 1953	
Squid, *Watasenia scintillans*	Wilke et al. 1953	
Squid, *Omnastrephes sloani pacificus*	Hotta et al. 1969	Wilke and Nicholson 1958
Northwestern Pacific and western Bering Sea:		
Sockeye salmon, *Oncorhynchus nerka*		Mizue et al. 1966
Unidentified small fish		Koga 1969
Unidentified fish		Mizue and Yoshida 1965; Mizue et al. 1966
Squids		Mizue and Yoshida 1965; Mizue et al. 1966; Koga 1969
Shrimp		Mizue and Yoshida 1965; Mizue et al. 1966; Koga 1969

northward in the summer to the Gulf of Alaska; it ranges the western North Pacific Ocean, from Japan northward to the Kurile Islands (National Marine Fisheries Service 1978). During pelagic fur seal research voyages off California (1958-66) and Washington (1958-72), 767 pods of dolphin totalling 8,803 animals were sighted[1] (297 pods, 5,555 dolphin, and 490 pods, 3,248 dolphin, respectively). Dolphin pod size ranged from 1 to 1,000+ animals. The dolphin reported here were collected from pods ranging from 4 to 300 animals.

The Dall's porpoise ranges the North Pacific Ocean from northern Baja California and Japan in the south to the Bering and Okhotsk Seas, moving into the southern portion of its range during winter. The porpoise usually occur in smaller groups than do the dolphin. During pelagic fur seal research cruises off California and Washington, 868 pods totalling 3,575 porpoise were sighted (657 pods, 2,845 porpoise, and 211 pods, 730 porpoises, respectively). Porpoise pods generally contained fewer than 20 animals. The porpoise reported here came from pods of three to five animals. Sightings and collections of dolphin and porpoise were obtained during 388 d at sea off California in 1958-66 and 368 d at sea off Washington in 1958-72.

The northern fur seal ranges across the subarctic waters of the North Pacific Ocean and numbers about 1.8 million animals (Lander and Kajimura 1976). Most seal are found near their breeding islands in the Bering and Okhotsk Seas from July into early November except for the very small San Miguel Island, Calif., population that numbers about 2,000 animals. In the eastern North Pacific Ocean few adult males are found south of the Gulf of Alaska. Mature females and immature males and females begin to appear in coastal waters between British Columbia and central California in late November and early December, the pups slightly later in January or February. The movement is generally southward along the continental shelf and slope in January into March with some animals ranging south to about lat. 32° N; however, most of the wintering population can be found between about lat. 35° and 49° N. Some northward migration out of this region may begin as early as March. Most wintering seal are found from over the continental shelf seaward as much as several hundred miles (Fiscus 1978).

Northern fur seal are most frequently observed alone rather than in company with other seal of their species; however, concentrations do occur in areas of abundant food supply. In 1966 (January-March) off California when most of the dolphin and porpoise were collected, 1,441 groups of seal were observed, of which 31% were single animals; 22% were in groups of 2; 16.9% in groups of 3; 10.5% in groups of 4; and 10.2% in groups of 5-20 (Marine Mammal Biological Laboratory 1969).

In 1967-68 (November-February) off Washington, when most of the dolphin and porpoise were collected, 669 groups of seal contained 40.8% single animals; 24.9%, groups of 2; 13.6%, groups of 3; 9.3%, groups of 4; and 14%, groups of 5-9 (Marine Mammal Biological Laboratory 1970).

There are no reliable estimates of the numbers of Pacific white-sided dolphin and Dall's porpoise that inhabit the eastern Pacific offshore waters from California to Washington; however, these two species are the most frequently sighted cetaceans in these waters.The northern fur seal is the only pinniped regularly inhabiting this region. It is a seasonal visitor, from December through May; as many as 500,000 may be here during the peak of the wintering period (Fiscus 1979).

Methods

Hand harpoons or shotguns were used to collect the Pacific white-sided dolphin and Dall's porpoise as they rode the bow wave of the research vessel or dory. Northern fur seal were collected from the vessel or dory with shotguns. The dolphin and porpoise were taken off California, 1-130 km seaward of the continental shelf; those from Washington waters were taken near or over the continental shelf.

Standard measurements and weights of each cetacean and seal were recorded (American Society of Mammalogists, Committee on Marine Mammals 1961, 1967). Reproductive tracts, skulls, stomachs, and tissue samples were collected. Stomachs were tied with string at the esophagus and pyloris and then injected with and preserved in 10% Formalin[2] for laboratory examination. The contents of each stomach were gently washed and drained in a small mesh sieve. The stomach rugae

[1]NMFS, Natl. Mar. Mammal Lab. 1958-74. Birds and mammals observed at sea. Unpubl. data listing, various pagination. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

were carefully checked for squid beaks, fish otoliths, and other small remains of food items. After excess fluid was drained off, the total weight of stomach contents was recorded and a total volume determined by water displacement. Individual food items were identified, counted, and the percentage of the total volume represented by each type of food item estimated. Fragments of prey species may remain in the stomachs of these animals from 12 to 24 h after feeding; hence hard parts of prey species consumed over the shelf, such as chitinous beaks of squids, fish otoliths, and particularly dense fish bones, may still persist in the stomachs of animals taken well offshore of the shelf. Identification was made by comparison with reference specimens and to descriptions in taxonomic keys or other references.

Of the 33 dolphin taken off California, 25 were females (9 adult, 15 subadult, 1 probably adult) and 8 were males (3 adult, 5 subadult). Of 11 dolphin taken off Washington, 8 were females (2 adult, 6 subadult) and 3 were males (1 adult, 2 subadult). All nine of the Dall's porpoise were adults.

Scientific names of marine mammals follows Marine Mammal Commission[3]; of fish, Bailey et al. (1970) and Fitch and Lavenberg (1971); of cephalopods, Young (1972).

Results

Pacific White-Sided Dolphin and Northern Fur Seal

Northern anchovy, *Engraulis mordax*, was the most frequently occurring fish in the stomachs of white-sided dolphin and northern fur seal taken in all collection months and across the latitudinal range of the collections off California. Most dolphin were taken off central California between Pt. Conception and Pt. Reyes in the following numbers by month: 1 in January, 11 in February, 18 in March, 2 in June, and 1 in December. Seal used in comparisons were taken in the same localities at the same times. Northern anchovy remains were identified from 58% (19 occurrences) of the dolphin stomachs and 32% (13 occurrences) of seal stomachs collected in the same localities.

Pacific whiting, *Merluccius productus*, was found in 33% (10 occurrences) of the dolphin stomachs and 34% (14 occurrences) of the seal stomachs. Pacific whiting was particularly important in the March 1966 collections at lat. 35° to 38° N (Morro Bay to San Francisco). Pacific saury, *Cololabis saira*, the third ranking fish, was found in 28% (9 occurrences) of the dolphin but in only 7% (3 occurrences) of the seal from the same area.

Squids of the family Gonatidae were the most frequently occurring cephalopods. Both *Loligo opalescens* (64% occurrence) and *Onychoteuthis borealijaponicus* (45% occurrence) were found in the dolphin stomachs in trace amounts only (beaks); however, both species are important seal prey. *Abraliopsis* sp. was identified only once in seal but found in 16 dolphin stomachs from seven collection locations off California. Stomachs of the nine dolphin collected 25 February 1966 off Pt. Reyes contained a greater variety of fishes and squids than those collected in other locations.

The food items consumed by 11 dolphin and 14 seal collected in the same locality off Washington show salmonids, *Oncorhynchus* spp., composed most of the stomach contents of 10 dolphin and 12 seal taken 25 and 26 February 1968 over the Astoria Canyon, approximately 37-44 km west of the Columbia River (8 occurrences in dolphin, 3 in seal). Flatfishes (Pleuronectidae) were present in one seal stomach. Squid beaks representing nine families, genera, or species of squids were identified from the stomachs of dolphin, but these taxa were of minimal importance in the stomachs of seal collected from the same area, occurring in only 4 of 12 stomachs. One dolphin, taken off the continental shelf, 25 April 1972, contained trace amounts of unidentified fishes and squids representing at least five genera. The stomachs of two seal collected in the same area the same day were empty.

Dall's Porpoise and Northern Fur Seal

The stomach contents of 9 Dall's porpoise and 17 northern fur seal taken from the same location off California and Washington from 1964 to 1968 were examined. One porpoise was taken in January off southern California and four were taken in February and one in April off central California. Three were taken off Washington, two in January (one taken in the entrance to the Strait of Juan de Fuca) and one in February. Off California, northern anchovy, Pacific whiting, Pacific saury, and squids, *L. opalescens* and *O. borealijaponicus*, formed major portions of the most recent feedings.

[3]Marine Mammal Commission. 1976. Marine mammal names. Unpubl. manuscr., 8 p. Marine Mammal Commission, 1625 Eye Street, NW., Wash., DC 20006.

Unidentified fishes and six species of squids were also found in trace amounts. The stomachs of three porpoise taken 56 km southwest of Pt. Reyes on 21 February 1966 contained no northern anchovy but did contain typical open ocean dwelling fishes and squids. Off Washington trace amounts of eulachon, *Thaleichthys pacificus*; rockfish, *Sebastes* spp.; sablefish, *Anoplopoma fimbria*; flatfish, Pleuronectidae; American shad, *Alosa sapidissima*; capelin, *Mallotus villosus*; and squids, *L. opalescens*, Gonatidae, *Gonatus* sp., and *O. borealijaponicus*, were found in stomachs of three porpoise.

Discussion

Distribution of Prey

Based on identified prey species, it appears that all three of the mammals feed in the epipelagic (0-200 m) and mesopelagic (200-1,000 m) zones of the ocean and that over the continental shelf, they may descend to the bottom (200 m or less) on occasion as demonstrated by the presence of demersal species in their stomachs. Many of the fishes and squids rise to or toward the surface at night, thereby becoming more readily available and perhaps ruling out the necessity for long, deep dives. Kooyman et al. (1976), reporting on fur seal diving behavior, indicated that dives between the surface and 20 m lasting <1 min may be for shallow feeding or travel and that dives between 20 and 140 m of 3.3-3.4 min duration may be hunting and feeding dives. They reported dives deeper than 140 m; the deepest reported dive lasted 5.4 min and reached 190 m. A study of blood oxygen levels of three genera of porpoise by Ridgway and Johnston (1966) reported that the Pacific white-sided dolphin cannot swim as fast and probably cannot dive as deep as the Dall's porpoise.

Prey Species

Off the California coast all three of the mammals feed primarily on small schooling fishes and cephalopods, including the northern anchovy, Pacific saury, and Pacific whiting. Other species of fish were probably taken as the opportunity arose. The primary fish species in dolphin collected off the Washington coast were salmonids (genus *Oncorhynchus*). Because the latter collection was made in a small area over a 3-d period, the taking of salmonids may have been opportunistic and short term rather than typical of more routine feeding. This sample is too small to conclude that a major predator-prey relationship exists between the Pacific white-sided dolphin and the salmonids.

Cephalopods are probably more important as prey species than indicated by the relative volume of stomach contents in the collection. Except for the chitinous beaks, cephalopods are probably more rapidly digested than fish. Marine mammals are more likely to feed on squids during the night because the vertical migration of many species brings them closer to the surface waters (Roper and Young 1975; Pearcy et al. 1977). Collection of dolphin during the day would give adequate time for digestion of fleshy parts, thus leaving the large numbers of indigestible chitinous beaks often found in stomachs.

The fishes and squids identified in the stomachs of the dolphin, porpoise, and seal taken during this study are presented in Table 2.

Stomach Capacity of Predators

The 44 Pacific white-sided dolphin were all adult or subadult animals, presumably with stomachs of maximum size. Eleven stomachs contained only trace amounts of food, and 33 contained food contents varying from 10 to 3,490 cm^3 (10-3,745 g).

The dolphin whose stomach contained the most food from California waters had eaten 68 anchovy (1,770 cm^3 or 1,895 g). Anchovy grow to 18-20 cm and may weight 57 g (Fitch and Lavenberg 1971).

Off Washington, the largest dolphin stomach examined contained the remains of nine salmon (including identifiable remains of four coho salmon and two pink salmon) which measured 26.0, 27.0, 31.0, 31.5, 31.5, 33.0, 33.0, 33.0, and 33.5 cm. The full stomach measured 40 cm long and 24 cm at the widest point (outside stomach dimensions), and the stomach contents represented 4.4% (3,490 cm^3 or 3,745 g) of the total body weight of the animal.

The largest stomach content from a Dall's porpoise off California contained 58 northern anchovy (1,000 cm^3 or 1,090 g). Off Washington, the largest stomach content contained fragments of five capelin, four eulachon, one flatfish (family Pleuronectidae), and trace amounts of squids (*Gonatus* sp. and Gonatidae) (130 cm^3 or 125 g). Five stomachs contained food volumes varying from 5 to 1,000 cm^3 (5-1,090 g) whereas four stomachs contained only trace amounts of food. Except for occasional

TABLE 2.—Size of fish and frequency of occurrence of fishes and cephalopods found in the stomachs of Pacific white-sided dolphin, Dall's porpoise, and northern fur seal[1] collected off California and Washington, 1964-72.

Taxon	Measurable length of fish in stomachs[2] (cm)	California			Washington		
		White-sided dolphin (33 coll.)	Dall's porpoise (6 coll.)	Northern fur seal ([3]41[4]10 coll.)	White-sided dolphin (11 coll.)	Dall's porpoise (13 coll.)	Northern fur seal ([3]14[4]7 coll.)
Fish:							
Pacific lamprey, *Entosphenus tridentatus*[5]	—	—	—	—	1	—	—
American shad, *Alosa sapidissima*	—	—	—	—	—	—	1
Pacific herring, *Clupea harengus pallasi*	28.5-31.3 (11)	—	—	—	—	—	—
Northern anchovy, *Engraulis mordax*	14.5-17.8 (19)	19	2	[3]13[4]5	—	—	—
Salmon, *Oncorhynchus* spp.[5]	—	—	—	—	8	—	2
Pink salmon, *O. gorbuscha*[5]	25.0-40.5 (3)	—	—	—	—	—	2
Chum salmon, *O. keta*[5]	—	—	—	—	1	—	1
Coho salmon, *O. kisutch*[5]	21.0-33.0 (5)	—	—	—	2	—	2
Chinook salmon, *O. tshawytscha*[5]	21.0-24.5 (2)	—	—	—	—	—	—
Capelin, *Mallotus villosus*	10.9-15.5 (26)	—	—	—	—	1	—
Eulachon, *Thaleichthys pacificus*[6]	15.3-20.5 (4)	—	—	—	—	1	1
California lanternfish, *Symbolophorus californiensis*[5]	—	1	—	—	—	—	—
Pacific saury, *Cololabis saira*[6]	—	9	1	3	—	—	—
Pacific whiting, *Merluccius productus*	—	10	2	[3]14[4]1	—	—	—
King-of-the-salmon, *Trachipterus altivelis*[5]	—	1	—	—	—	—	—
Jack mackerel, *Trachurus symmetricus*	—	1	—	—	—	—	—
Drum, *Sciaenidae*	—	—	—	1	—	—	—
Medusafish, *Icichthys lockingtoni*[5]	—	1	—	—	—	—	—
Rockfish, *Sebastes* spp.[5]	—	1	—	1	—	—	2
Sablefish, *Anoplopoma fimbria*	25.0 (1)	—	—	—	—	—	1
Pacific sanddab, *Citharichthys sordidus*[5]	—	1	—	—	—	—	—
Righteye flounder, Pleuronectidae[6]	—	—	—	—	—	1	1
Cephalopods:							
Squid, *Loligo opalescens*		21	1	[3]2[4]1	3	1	
Squid, *Abralia*[5]*opsis* sp.[5]		16	3	1	11	—	—
Squid, *Octopoteuthis* sp.[5,6]		12	1	—	9	—	—
Squid, Gonatidae		14	2	[3]1[4]2	11	2	[3]1[4]2
Squid, *Gonatus* sp.		23	1	2	11	2	3
Squid, *Gonatopsis borealis*[5]		7	—	—	2	—	—
Squid, *Onychoteuthis borealijaponicus*[5]		15	2	4 1	11		1
Squid, *Chiroteuthis* sp.[5]		2	—	—	3	—	—
Squid, *Cranchiidae*[5]		3	1	—	3	—	—
Pelagic octopus, *Ocythoe tuberculata*[5]		2	—	—	—	—	—

[1]A complete list of prey species of the northern fur seal appears in North Pacific Fur Seal Commission Reports on Investigations, 1962, 1969, 1971, 1975.
[2]Length measurement of chinook salmon and sablefish is standard length, other measurements are total length. The numbers in parentheses indicate sample size.
[3]Northern fur seal in association with Pacific white-sided dolphin.
[4]Northern fur seal in association with Dall's porpoise.
[5]Identified for the first time as prey of the Pacific white-sided dolphin.
[6]Identified for the first time as prey of the Dall's porpoise.

squid beaks, bone fragments, and otoliths, which were found in the fundic (or pyloric) stomach and the duodenal ampulla, all undigested or semidigested food items were found in the forestomach. Stomach volumes were highly variable depending on the time of day the animal was collected and the digestibility of the species of fish or squid ingested. Of 30 dolphin taken off California, those taken before 1000 h averaged more than twice the volume of food in their stomachs than those taken after 1000 h.

During the course of pelagic fur seal research, thousands of seal stomachs have been examined by the authors. The stomach containing the most food was from a 17-yr-old male collected in the eastern Bering Sea at 1330 h, 9 August 1968. The animal had consumed 13 walleye pollock, *Theragra chalcogramma*, and 4 squid, *Berryteuthis magister*. The contents weighed 9.8 kg (9,175 cm^3 volume representing 7.2% of body weight) with walleye pollock composing 80% (7,340 cm^3) of the total stomach volume. The stomach of an adult female fur seal contained food weighing 5.9 kg (5,565 cm^3 volume representing 13.1% of body weight). This 15-yr-old animal was collected at 0645 h on 19 April 1964 off California and had fed on 31 Pacific whiting.

The energy requirements of the northern fur seal are poorly known. Keyes (1968) reported that seal and other pinnipeds kept in captivity subsisted well on 6-12% of body weight daily, with vitamin supplements. Studies indicate possibly higher daily consumption rates among growing immature animals. Sergeant (1969) summarized the feeding rates per day of several captive cetaceans including two dolphin which consumed 7.9% of their body weight in herring and mackerel and a porpoise that consumed 11.3% of its body weight of mackerel. Ridgway (1972) reported food requirements in captive animals equalled 7-8% of body

weight/d for dolphin and 10-12% for porpoise. The species fed to these captive animals were not identified.

Size of Prey

Higgins (1919) mentioned a stomach containing six large Pacific sardine, *Sardinops sagax*, each about 30 cm long. Houck (1961) reported a dolphin with a stomach full of Pacific saury and with a 33 cm jack mackerel, *Trachurus symmetricus*, wedged in its throat. Unfortunately, no count of the Pacific saury was given. Fitch and Brownell (1968) reported that otoliths representing 29 Pacific whiting 40-50 cm long and 14 Pacific whiting about 20 cm long were recovered from a dolphin stomach. The sizes of fish in stomach contents were measured only from whole or nearly whole specimens or those with complete vertebral columns (Table 2). All salmon consumed by dolphin were generally immature, showing 0-age ocean growth, although a few showed 1, 2, and 3 ocean annuli.

Scheffer (1953) reported on stomach contents of two Dall's porpoise taken off Oregon, each of which contained four Pacific whiting about 45 cm long. These records represent the largest fish recovered from porpoise stomachs. Mizue et al. (1966) reported only one occurrence of sockeye salmon, *O. nerka*, from stomachs of 148 porpoise taken in conjunction with the high-seas salmon gill net fishery. No mention was made of the size of this fish, although they did state that adult salmon are probably not taken by animals of this species.

In our collections, there was no evidence of large fish being broken up prior to ingestion by either dolphin or porpoise. Captive bottlenose dolphin, *Tursiops truncatus*, have been observed to break up food species.[4] The teeth, jaw structure, and relative neck mobility of the white-sided dolphin are similar to those of the bottlenose dolphin and would allow such behavior in this species more so than in the Dall's porpoise. The maximum size of prey eaten is apparently limited by the predator's ability to capture and swallow whole fish.

The size of prey listed in Table 2 does not necessarily indicate that these fish are the largest consumed by the seal. Seal generally swallow smaller fish and squid whole below the surface whereas larger fish are brought to the surface and broken into smaller pieces by grasping them with their teeth and shaking them violently from side to side. The largest fish we have seen taken by a seal was a king-of-the-salmon (length 170 cm) which we took away from the animal as it attempted to break the fish into smaller pieces at the surface.

[4]William Gilmartin, Naval Ocean Systems, San Diego, Calif., pers. commun. 1978.

Conclusions

The Pacific white-sided dolphin and the Dall's porpoise feed primarily on small schooling fishes and cephalopods. They, like the northern fur seal, are opportunistic feeders, preying on available species, including some that are commercially important such as salmon, anchovy, jack mackerel, and *Loligo opalescens*. Meaningful estimates of the dolphin and porpoise populations are unavailable, and too few stomachs have been examined to make any estimate of the percentage of commercially important fishes included in the diet.

Regardless of the time of day collected, stomachs may contain undigested fish indicative of recent feeding. Based on stomach content volume and time of collection, large stomach volumes were most often observed in animals collected before 1000 h in the morning, indicating that most feeding is done at night or in the morning.

Northern fur seal tend to congregate in areas of abundant food supply and usually feed at night, probably because most prey species rise toward the surface after dark and are more readily available (Fiscus et al. 1964). Food species consumed by the seal vary by area, but the important food in the diet of this mammal in a given area, based on percentage of stomach content volume, generally does not change—only ranking by volume changes. The animals collected on the continental shelf appear to feed on fishes, whereas those taken beyond the shelf feed primarily on squids.

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SPAWN AND LARVAE OF THE PACIFIC SANDFISH, *TRICHODON TRICHODON*

Little is known about the biology of the Pacific sandfish, *Trichodon trichodon*, other than that the adults are characteristic of inshore, sand-gravel communities (Isakson et al. 1971); they occur from San Francisco, Calif., to Kamchatka, USSR (Hart 1973); and they burrow into a sandy substrate (Clemens and Wilby 1961). Clemens and Wilby reported that a mature female taken on Long Beach, Vancouver Island, Canada, extruded mature eggs (upon disturbance) in February.

The first discovery of natural spawn of *T. trichodon* and subsequent rearing of larvae through metamorphosis at the Vancouver Public Aquarium has provided information about the reproduction and early life history of this species. In addition to life history notes, this paper presents a description of larvae of *T. trichodon*.

Methods

A portion of an egg mass was collected at lat. 48°56′ N, long. 125°43′ W, 16 km southeast of Long Beach, Vancouver Island, on 12 June 1976 and transported in a plastic bag with oxygen and seawater to the Vancouver Aquarium, where it was incubated in an aerated aquarium with seawater (25-29‰, 8°-13° C) provided at an inflow rate exceeding 100 tank volumes/d. The seawater temperature changed seasonally with changes in average ambient seawater surface temperatures, so that the salinity/temperature regime was comparable with that which the eggs would have encountered intertidally. The eggs were fixed in a bag of nylon mesh in front of the inlet pipe. In October, December, and January, embryos were excised from a few of the eggs to determine whether development was continuing. About once per month egg membranes were scrubbed with a bottle brush to remove diatom growth.

As they hatched the larvae were collected with a beaker and transferred to a 1,000 l rearing tank (ca. 1 m depth × 1 m in diameter) with seawater (25-27‰, 10°-12° C) inflow at a rate exceeding one tank volume per day and a light cycle of 14 h light and 10 h dark, including simulated twilight periods. Larvae were provided brine shrimp, *Artemia salina*, nauplii daily in excess quantities. Debris was siphoned from the tank bottom daily and examined for dead fish larvae. Juveniles were placed in a tank with a sand bottom and flow-through seawater and were fed frozen euphausiids and frozen brine shrimp.

At various ages specimens were preserved in 3% Formalin[1] in seawater, with borax and Ionol. Freshly killed specimens were measured to the nearest 0.5 mm standard length (SL), then measured again 1 yr after preservation, to determine shrinkage. Line drawings, morphometric data, and meristic characters were based on preserved specimens.

Life History Notes

The egg mass was found in a surge channel on a rocky shoreline between 0.6 and 1.0 m tide levels. The mass was visually estimated to have about 1,000 eggs, was irregularly shaped, and adhered firmly to the rock surface.

Adults of this species are known to inhabit sandy beaches, whereas the egg mass is suited only to rocky substrate to which it can adhere. Presuming an incubation period of about 1 yr as discussed below, most plant substrates would be too ephemeral for an egg deposition site and bedrock on sand beaches could be covered by seasonal shifting of sand. Rocky shoreline removed from sandy areas would therefore provide the most stable substrate for the adhesive eggs. The precise location on the wall of a fully exposed surge channel might provide a refuge from egg predation as well as high flow velocities for gas exchange. The rocky intertidal area in which this egg mass occurred is located 8 km from the nearest sandy intertidal area. Thus, a limited spawning movement along the shore must occur.

[1]Reference to trade names does not imply endorsement by the Vancouver Aquarium or by the National Marine Fisheries Service, NOAA.

The *T. trichodon* eggs were amber colored and large in size (3.52 mm in diameter ±0.10 SE, n = 17 eggs), and slightly flattened at points of attachment. About 25% of the collected eggs were dead at the time they were taken. When collected the embryos had developed both melanic choroid pigment and guanine iris pigment on the eyes.

Considering the state of development of these embryos, it was expected that these eggs would mature and hatch within a month after collection, since benthic egg masses of many northeast Pacific fishes mature to hatching within 1 to 3 mo after fertilization (pers. obs. on 28 species). The *T. trichodon* eggs, however, continued to develop for over 8 mo after they were collected, then all hatched within a 24-h period.

As a basis for comparison, wolf-eel, *Anarrhichthys ocellatus*, eggs are large (ca. 5 mm in diameter) and have a relatively long incubation of 3 mo at 10°-12° C (pers. obs. on captive spawn). At 1 mo after fertilization (one-third of incubation period), *A. ocellatus* embryos reach a developmental state comparable with that of the *T. trichodon* at the time of the collection, with pigmented eyes on an embryo still many times smaller than the yolk sac. Assuming comparability in relative rates of development, a full incubation period of 12 mo could therefore be calculated for the *T. trichodon*. An incubation period of 1 yr would indicate February as the time of spawning, which coincides with the finding of a ripe female in February in the same area of Vancouver Island (Clemens and Wilby 1961).

About 90% of the hatch occurred within 4 h, in late afternoon, the remainder the next morning. The *T. trichodon* eggs had not been handled for 2 wk prior to hatching and no other fish eggs had hatched in the incubation tank for a week prior to this hatch, so it appears unlikely that this abrupt hatch was unnaturally stimulated. Only a few egg mortalities occurred during the incubation period in the laboratory; this low egg mortality, together with the occurrence of an abrupt and fully viable hatch, indicates that the observed incubation period was normal for this species, as an abnormal incubation should adversely affect viability. Although incubation periods of about 1 yr have been reported for an unrelated fish species, *Agonus cataphractus* (see Breder and Rosen 1966 for review), such prolonged incubation is evidently rare.

The larvae were reared in the laboratory from hatching through metamorphosis with no mortalities (maximum age 29 mo, 137 mm SL). Larvae hatched on 15 and 16 February 1977 at 14.5 mm SL (16 mm TL) and grew to 40-43 mm SL (45-50 mm TL) in 70 d, by which time the fish resembled small adults. Allometric growth in the deeping and lateral compression of the ventral body continued to about 50 mm SL, along with upturning of the jaw and development of fringed lips, as shall be discussed in the following section.

Immediately upon hatching the larvae swam to the water surface and began schooling at the surface in a two-dimensional array (one-fish deep). This neustonic schooling behavior shifted to a pattern of subsurface schooling (three-dimensional schools, usually within 10 cm of the surface) at about 48 h after hatching. At this time, feeding was first noted. By 72 h after hatching, about half the larvae had food in the guts within 4 h of the daily food introduction; about 80% had full guts after introduction of food on day 4 (96 h). Schooling behavior was characteristic of the entire period of larval development; these schooling tendencies decreased progressively during metamorphosis (from about 30 to 50 mm SL) and the juveniles did not show true schooling behavior in the confines of aquaria.

The larval *T. trichodon* were rapid swimmers. Alexander (1967) mentioned 10 body lengths/s as a maximum burst speed for teleosts of any size and 3-5 body lengths/s as a maximum sustained speed (maintained for at least several minutes). Although no effort was made to determine precisely the cruising speed of larval *T. trichodon*, observations of the distance traversed in 5 s intervals revealed a cruising speed of about 10 body lengths/s and always over 5 body lengths/s. This rapid swimming occurred abruptly upon hatching, before the onset of feeding. Synchronized hatching, the abrupt onset of schooling, and rapid swimming may have evolved as mechanisms for larvae to escape the physical dangers of the wave-swept incubation site.

Trichodon trichodon first burrowed into sand as metamorphosed juveniles of 50-60 mm SL. They burrowed by simultaneously undulating the body laterally while fanning the pectoral fins upward and forward, so that the body sank downward and backward into the sand. The eyes and nostrils usually remained exposed above the sand, although the entire body could be buried. Burrowing did not occur until fleshy fringes had developed on the jaws. The fringed lips may permit water to be inhaled without allowing sand to enter the buccal cavity. The allometric growth prior to inital bur-

rowing may indicate a functional role of the deep, narrow form of the ventral part of the body in burrowing.

Larval Development

Morphometric and meristic features of an excised embryo (2 wk prior to hatching) and larvae of nine posthatching ages are presented in Table 1. The outstanding feature of the late embryo was the presence of caudal fin rays and a flexing notocord with the posterior margins of the hypural plates about 45° to the horizontal body axis. This precocious development of the caudal fin remained a diagnostic character throughout the larval period and probably contributed to the rapid swimming speeds discussed earlier.

The late embryo and the newly hatched larvae have a large oil droplet positioned anteriorly in the yolk. The abdomen has about 40 melanophores radiating from the dorsal gut surface. In addition to the features detailed in Table 1, these early ages have a few external melanophores in the nasal region, lower jaw angle, cranial region (7-10), and anterior mandibles (Figure 1). There is also an internal melanophore anterior to each otic capsule and, in fresh material, about 30 xanthophores over the cranium. Three preopercular spines are present as are the pectoral fin rays.

By 9 d hatching age, the posterior margins of the hypural plates are approaching a vertical orientation and have an increased number of melanophores, while the caudal and pectoral fin rays have increased in length. There is a row of 4 or 5 small melanophores along each side of the anterior insertion of the dorsal fin fold and an internal row of about 24 melanophores along the notocord (less clearly visible than external pigment, therefore not illustrated). Eight small melanophores have appeared in the cranial region, clustered among six larger ones, previously developed. A single melanophore has appeared on the ventral midline of the lower jaw (not visible in side view). Rows of melanophores have also appeared along the anterior end of the mandibles and horizontally on the dorsal portion of the operculum. Snout melanophores become prominent by this stage, as do teeth on the lower jaw. These teeth are easily visible at this stage, becoming progressively reduced until, at 25 d hatching age, they are no longer noticeable.

The 18-d specimen has vertical posterior margins on the hypural plates, a forked caudal fin, and

TABLE 1.—Count and morphometric data during early development of *Trichodon trichodon*. Fresh length, immediately after killing; preserved length, 1 yr later.

Hatched age (d)	Fresh length (mm SL)	Preserved length (mm SL)	SL, percent shrinkage	Preserved snout-anus length (mm)	Ratio snout-anus ÷ SL	Preserved body depth (mm)	Ratio body depth ÷ SL	Myomeres		Fin ray counts				Melanophore count	
								Preanal	Postanal	D-1	D-2	Anal	Pectoral	Pelvic	PVM[1]	Hypural
Embryo	—	11.0	—	—	—	—	—	12	36	0	0	0	—	0	16	3
0	14.5	13.0	10.3	4.5	0.35	2.5	0.19	12	38	0	0	0	—	0	18	3
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	38	0	0	0	—	0	16	1
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	40	0	0	0	—	0	20	2
9	—	14.5	—	5.0	0.34	3.0	0.21	12	37	0	0	0	—	0	16	4
18	19.5	17.2	11.8	7.0	0.41	3.3	0.19	12	37	0	0	0	21	0	20	6
25	21.0	20.0	4.8	8.7	0.43	4.2	0.21	14	34	VIII	15	28	21	0	18	Bands
29	24.5	22.0	6.1	9.3	0.42	5.0	0.23	15	34	X	19	27	21	0	[2]19 + 19	Bands
35	27.5	27.0	1.8	12.0	0.44	5.5	0.20	14	32	XII	18	I,28	21	3	19 + 21	Bands
43	29.0	28.0	3.4	12.7	0.45	6.8	0.24	15	34	XIII	18	I,28	21	I,3	25	Brackets
56	31.5	30.0	4.8	14.0	0.47	7.0	0.23	13	35	XIV	19	I,29	23	I,5	19	Brackets
56	32.5	32.0	1.5	15.0	0.47	7.0	0.22	14	36	XIII	18	I,28	21	I,5	20	Brackets
70	40.0	38.0	5.0	18.0	0.47	9.3	0.24	14	36	XIV	I,19	I,29	22	I,5	15	Brackets
70	43.0	40.5	5.8	20.5	0.51	11.0	0.27	14	34	XIV	I,17	I,27	22	I,5	12	Brackets

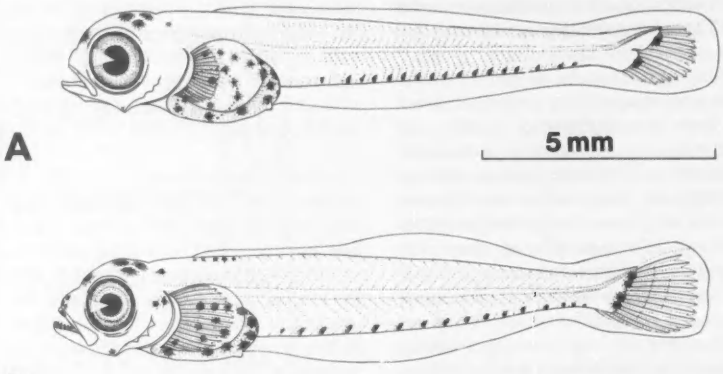
[1]Postanal ventral midline melanophores versus hypural melanophores.
[2]Internal and superficial melanophore counts.

secondary caudal fin rays. Melanophores are more numerous along the insertion of the dorsal fin fold (18-19 each side), internally along the notocord (27; vague, not illustrated), along the ventral midline of the lower jaw (10), in the cranial region (7 large, 23 small), and on the posterior margin of the hypurals (6). Melanophores appear larger and more dense on the dorsal gut surface as well. Two melanophores are present laterally at the angle of the notocord and 10 melanophores are visible on the principal caudal rays. Pectoral fin ray development is complete (21 rays) and four preopercular spines are evident.

By 25 d hatching age the melanic pigmentation of the dorsal body surface, jaw, and snout has proliferated considerably, while dorsal and anal fin ray development has started (Table 1) and pelvic fin buds are visible. Paired rows of 38 large melanophores occur on the dorsal body along the entire length of the dorsal fin. Cranial melanophores appear as a pair of dense patches (one on each side) with a third median patch on the nape region. The postanal ventral midline melanophores appear more internal than at younger ages. A new row of superficial melanophores has appeared on the mediolateral trunk musculature (posterior half of body), while the angle of the notocord is overlaid by an angular "bracket" of small melanophores, the dorsal leg of which continues anteriorly as a faint internal row dorsal to the notocord. The melanophores at the posterior margin of the hypurals form continuous vertical bands on each plate. Finally, a fifth preopercular spine is becoming visible ventrally.

The 29-d specimen (not illustrated in Figure 1) is marked by the appearance of a ring of small melanophores around each eye, the development of both internal and superficial ventral midline melanophores (Table 1) and doubled rows of melanophores along each side of the dorsal fin base on the anterior half of the body. Cranial and dorsal gut melanophores have continued to become more dense and the pelvic fins are formed, without elements.

At 35 d hatching age, melanophores are on the dorsal margin and dorsal insertion of the pectoral fin and melanophores are arrayed in double or triple rows on each side of the dorsal fin bases



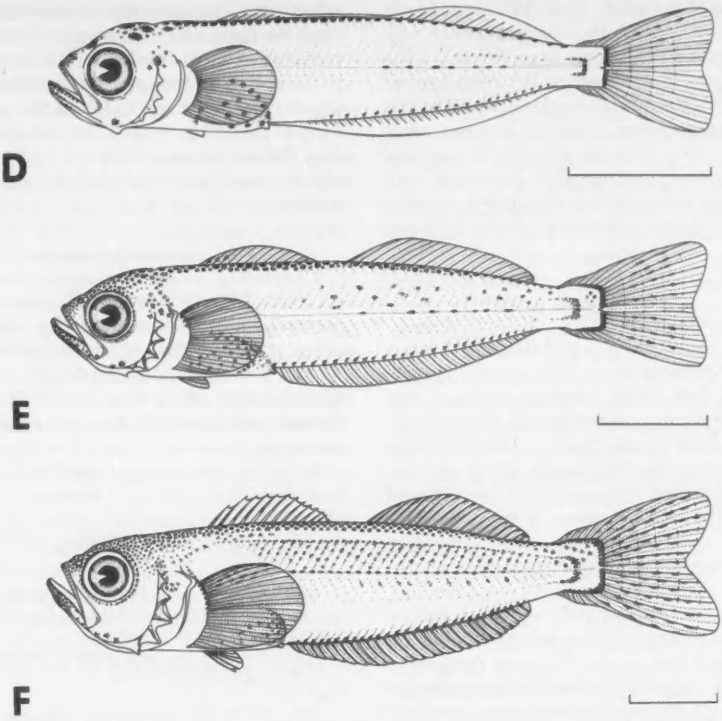


FIGURE 1.—Larvae and early juveniles of *Trichodon trichodon* (preserved lengths). A. 0 d, 13 mm SL; B. 9 d, 14.5 mm SL; C. 18 d, 17.2 mm SL; D. 25 d, 20 mm SL; E. 35 d, 27 mm SL; F. 56 d, 32 mm SL.

posteriorly to the middle of the second dorsal, continuing as single rows across the peduncle. Melanophores are on the first three elements of the first dorsal fin. On the lower jaw, melanin has extended posteriorly to the juncture with the maxillaries. A patch of melanophores has developed on the dorsal preoperculum. About 26 scattered melanophores appear dorsolaterally on the trunk musculature, above the mediolateral row, and melanophores occur closely spaced, lining the edges of principal caudal rays. The melanophores on the hypural margins have spread anteriorly along the insertion of the secondary caudal rays. Allometric growth at this age includes an increase in the relative snout-anus length (Table 1) and a slight upturning of the jaw.

The 43-d specimen (not illustrated) exhibits more regular arrays of the most recently developed melanophore patterns: the mediolateral row consists of 33 melanophores, the dorsolateral melanophores now form broken rows along the margins of myomeres, and the caudal rays are lined with rows of melanophores. By this age, gut melanophores appear internal rather than external. Only superficial ventral midline melanophores (25) are visible.

The 56-d specimen is easily recognized as a young sandfish. The entire snout, jaw, cranium, and nape regions are densely covered with melanophores, continuous with rows along the dorsal fin bases. The upper pectoral fin rays are lined with melanophores, as are the spines on the anterior half of the first dorsal fin. More melanophores have appeared over the caudal peduncle. All fins are completely formed by this stage and the five preopercular spines appear to radiate from a centrum.

By 70 d hatching age the body proportions re-

semble those of the adult. Hart (1973) listed body depth as 0.28 SL for adults, which compares with 0.27 SL for the 70-d specimen (Table 1). The snout-anus length has reached the adult proportion of 0.5 SL (Hart 1973) by this stage. The jaw angle and eye position have not attained adult character by 70 d, however, and the fringed lips and elongate nostrils of the adult are not evident. These features are present by the time burrowing behavior first appears at sizes of about 55-60 mm SL (165 d).

Discussion

Larvae of *T. trichodon* are distinct and easily identified. Myomere counts alone would separate *T. trichodon* from other elongate larvae in the northeastern Pacific. As mentioned, the early development of the caudal fin is a distinguishing character of all early larval stages of *T. trichodon*. The newly hatched yolk-sac larva has a flexed notocord and developing caudal rays. The caudal fin is forked and has secondary rays developing prior to the development of elements of other median fins.

The melanophore patterns developed in gradual stages with little variation among the individuals from this particular hatch. The most distinctive melanophores are perhaps those in the caudal region, on the hypural margins, and at the notocord bend. The overall melanophore patterns for each stage could probably be used as a basis for diagnosis, certainly when taken together with the morphometry and fin development patterns.

The preopercular spines are present at hatching and seem unique among sympatric elongate larvae. The stellate arrangement of these spines in the later development stages is unique.

Altogether, there appears to be little chance for misidentification of this species in the northeast Pacific region. This is of interest in light of the absence of these larvae from records of ichthyoplankton surveys in this region (e.g., Richardson and Pearcy 1977). In the Gulf of Alaska, where *T. trichodon* is an abundant inshore fish species, only one larva has been taken by plankton nets in an extensive ichthyoplankton survey (Kendall[2]). The only other northeast Pacific larvae, of which I am aware, with such high-speed schooling in a laboratory situation are those of *Ascelichthys rhodorus* (pers. obs.), which also do not appear in plankton nets (Richardson and Pearcy 1977). Although this behavior may enhance evasive capabilities in areas sampled for plankton, a further possibility is that this behavior may enable larvae to inhabit the extreme nearshore, which is usually not included in regular plankton surveys.

[2]Arthur W. Kendall, Jr., Fishery Biologist, Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. August 1979.

Acknowledgments

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A RADIOLOGIC METHOD FOR EXAMINATION OF THE GASTROINTESTINAL TRACT IN THE ATLANTIC RIDLEY, *LEPIDOCHELYS KEMPI*, AND LOGGERHEAD, *CARETTA CARETTA*, MARINE TURTLES[1,2]

In the past 2 yr the National Marine Fisheries Service of the U.S. Department of Commerce has been raising hatchlings of the Atlantic ridley, *Lepidochelys kempi*, and loggerhead, *Caretta caretta*, marine turtles. These are classified as endangered and threatened species under the U.S. Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1977, 1978). The rearing activity was undertaken to provide a better understanding of the early life histories of those species.

Of immediate concern was the evaluation and treatment of skin, gastrointestinal, lung, and systemic diseases, which emerged rapidly in the captive turtles. Radiologic examination was sought as a possible diagnostic modality for various problems. To this end we have attempted to develop radiologic techniques for the study of normal and diseased animals.

In this paper we report on the use of barium sulfate contrast agent in studying the gastrointestinal (GI) tract of normal turtles and propose its use as an aid in the diagnosis of turtle GI diseases.

Methods

The GI tracts of two loggerhead and two ridley turtles, between the ages of 4 and 10 mo, were examined by means of commercially available 44% (wt/wt) aqueous barium sulfate suspension.[3] Similar suspensions are frequently used in the examination of the GI tract of humans (Margulis 1973; Miller 1973).

Preparation of the GI tract was accomplished by not feeding the animals for 2 d and then giving 0.5 ml of X-Prep, a commercial laxative of extract of senna fruit (Gray Pharmaceutical Company, Norwalk, Conn.), on the day prior to the examination. Next, the esophagus was intubated using a plastic umbilical artery catheter (Argyle, Cat. No. 8888-160-226, Sherwood Medical Co., St. Louis, Mo.) measuring 5 mm in circumference. The intubation of the ridley turtle's esophagus proved more difficult than the loggerhead's as they resisted passage of the catheter through the oropharynx. Therefore, a dose of 0.25 mg of succinylcholine chloride[4] was given subcutaneously in the neck to effect partial skeletal muscle paralysis. Paralysis was adequate in 4 or 5 min, rapidly diminished, and was nearly undetectable in 20 min. (No untoward side effects occurred.) Also, a plastic hollow guide (4 mm in diameter) was placed in the oropharynx and upper esophagus through which the umbilical artery catheter was threaded into the esophagus and stomach. Both the hollow guide and catheter were lubricated with small amounts of surgical lubricant. The placement of the catheter tip in the stomach and injection of approximately 5 ml of contrast material were done under fluoroscopic control. Radiographic films were then exposed using either the phototimed fluoroscopic filming device or manual techniques utilizing standard radiographic equipment, film, and film cassettes. The fluoroscopic unit, radiographic equipment, radiographic film, and film cassettes which were used are of standard medical grade and are available in most radiology departments. Serial filming consisting of fluoroscopic spot films, made in various degrees of obliquity and standard medical radiographic film[5] in cassettes (Halsey Rigidform, Halsey X-Ray Products, Brooklyn, N.Y.) equipped with par speed intensifying screens (Radelin TA-3, GAF Corp., Brooklyn, N.Y.), and industrial grade film[6] in cardboard cassettes made in the dorsoventral (DV) position were done on the day of the examination. For the following 2 d DV par speed medical films or industrial grade films were made on each consecutive day. Thereafter, DV films were exposed every other day for 4 d. Radiographic technique and film types are given in Table 1.

Radiation exposure using industrial film exposed at 60 kV peak and 400 mAs and par speed medical film exposed at 50 kV peak and 10 mAs with a target film distance of approximately 100 cm was 0.98 and 0.14 Roentgen/exposure, respectively. These measurements were obtained using a 0.6 cm^3 Baldwin-Farmer air ionization chamber

[1]The investigations involving the Atlantic ridley turtle were conducted under Permit No. PRT 2-1770 (U.S. Federal Fish and Wildlife Service), permits 1978-ABC-IV-0751, No. 27611-8786, and 1979-ABC-IV-1258, Exp. 4287 (Mexican Government).

[2]Contribution Number 81-1G, Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA.

[3]E-Z-EM Company, Cat. No. 750, Westbury, N.Y. Reference to trade names or commercial companies does not imply endorsement by the National Marine Fisheries, NOAA.

[4]Succinylcholine HCl injection U.S.P., Oraganon, Inc., West Orange, N.J.

[5]Kodak XRP-1, Eastman Kodak Co., Rochester, N.Y.

[6]Kodak RP/M, Eastman Kodak Co., Rochester, N.Y.

TABLE 1.—Radiographic technique for turtle examinations.

Weight (g)	Carapace length (cm)	Turtle position	Voltage (kV)	Current (mAs)	Tube-film distance (cm)	Film type
400	15.0	DV[1]	60	400	100	Industrial
300	12.5	DV	50-55	300-360	100	Industrial
350	13.5	DV	50	40	100	Industrial
400	13.0	DV	50	10	100	Medical
300-400	13-15	Variable	55-60	Phototimed (fluoroscopy unit)	—	Medical

[1]DV = Dorsoventral projection.

(Nuclear Enterprises, Inc., San Carlos, Calif.) on an electrometer[7] at 300 V collection potential.

Results

Adequate clearing of food residue was obtained after the subjects were prepared in the manner described in Methods. The experimental animals were quite small (0.3-0.4 kg) and good resolution and detail are a necessity if mucosal detail is to be adequately examined and appraised. Excellent detail of the esophagus, stomach, and small intestinal mucosa was obtained by using industrial grade film while adequate detail was obtained on par speed medical film. The radiologic anatomy of the esophagus, stomach, and small intestine correlated well with the findings noted at gross necropsy of turtles of similar age and size that had

[7]Model 602 Electrometer, Keithley Co., Cleveland, Ohio.

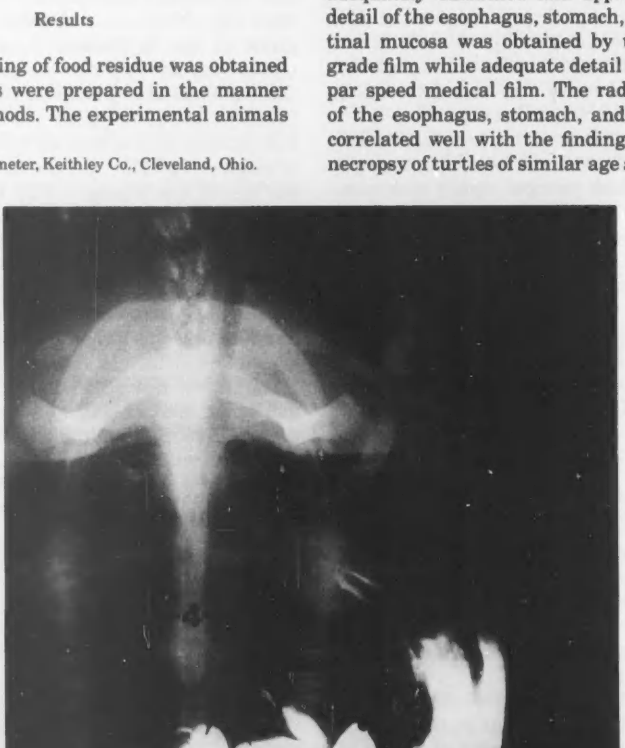

FIGURE 1.—Dorsoventral view of a 15 cm carapace length, 400 g, 8-mo-old loggerhead turtle made on the second day after barium instillation. Industrial grade film was used for this exposure. 1—stomach, 2—proximal small bowel, 3—tracheal air shadow, 4—lungs. The arrowheads demonstrate the longitudinal mucosal pattern in the proximal small bowel (1.8×).

died of various causes. Figure 1 shows the relatively smooth mucosa of the stomach which has been distended with barium. The smooth longitudinal folds of the proximal small bowel are also easily identified. Also in Figure 1 just to the left of the tracheal air shadow (3) and superimposed over the cervical vertebrae, a few esophageal papillae are faintly outlined by small amounts of barium. Incidently, injection of contrast directly into the esophagus demonstrated the esophageal papillae and the narrowing in the region of the gastroesophageal junction with greater clarity than in Figure 1. The size and position of the GI structures were also easily assessed. Continued filming over several days demonstrated slow progression of the barium sulfate suspension through the small intestine into the colon. In the colon residual fecal contents mixed with the barium and obscured the mucosal detail somewhat. Transit time was noted to be at least 4 or 5 d from the stomach to the proximal colon in all four animals studied.

Discussion

The radiologic examination of the upper GI tract of marine turtles by using barium sulfate as a contrast material provides a potential tool in the evaluation of various diseases in turtle populations. The radiographic information from these studies should aid in evaluating turtles for partial or complete small bowel obstruction, with associated changes in motility and bowel size, and foreign bodies within the intestinal tract such as parasites or bezoars. Diseases altering the mucosal pattern such as ulceration, gastritis, enteritis, or colitis caused by various infectious or inflammatory processes could be demonstrated. The disease states listed above are frequently demonstrated by similar GI studies performed in humans (Paul and Juhl 1972).

The use of succinylcholine chloride in these animals should be approached with caution. The total dose should be divided and given incrementally over 3-5 min until the desired effect is obtained. The use of a well lubricated plastic hollow guide is recommended prior to the decision to use a paralytic agent.

Radiation exposure was of concern but the calculated doses of 0.98 and 0.14 Roentgen/exposure for industrial and par speed medical film were well below the harmful radiation dose in several species of turtles found by Altland et al. (1951) and Cosgrove (1971). They resemble dosage levels used by Gibbons and Greene (1979), which produced no apparent harm to the freshwater turtles in their study. To reduce radiation exposure during the examination the use of par speed medical film which requires a lower radiation dose is recommended when the clinical situation permits. For instance, intestinal obstruction would require only par speed medical film technique, as demonstration of mucosal detail would be unnecessary when assessment of dilatation of the bowel, stasis of contents, and site of the obstructing process would be primary concerns. In examinations where mucosal detail is desirable such as detection of small ulcerations, industrial film and its attendant higher exposures may become necessary.

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SUMMER FOOD OF PACIFIC COD, *GADUS MACROCEPHALUS*, IN COASTAL WATERS OF SOUTHEASTERN ALASKA

The Pacific cod, *Gadus macrocephalus* Tilesius, is ecologically important in the Gulf of Alaska and may be more extensively utilized in future commercial fishing efforts. Although Pacific cod is one of the most abundant demersal fish in shallower (<200 m depth) waters of the Gulf of Alaska (Alverson et al. 1964; Ronholt et al.[1]), it has not been extensively fished. The total harvest of Pacific cod from the Gulf of Alaska (mostly by foreign fishing fleets) is estimated to be a "small fraction of the maximum sustained yield" and "substantially higher catches" could be supported (North Pacific Fishery Management Council[2]). Because of the recent establishment of the 200-mi United States Fishery Conservation Zone and a concurrent interest in bottomfishing, a domestic fishing industry may develop that could also exploit Pacific cod.

Little research has been done on the Pacific cod in Alaskan waters, especially concerning its foods. Most of the studies on Pacific cod have been conducted by Soviet investigators in the northwestern Pacific Ocean (summarized by Moiseev 1953). Jewett (1978) investigated the diet of Pacific cod near Kodiak Island, Alaska. In this note, I report the foods of Pacific cod in a different region of Alaska, southeastern Alaska.

Methods

Pacific cod were sampled during a cruise conducted by the National Marine Fisheries Service primarily to assess cod resources and evaluate different types of fishing gear used. During a 17-d period in July 1977, 520 Pacific cod stomachs were collected in two regions of southeastern Alaska coastal waters: 17 sites in the Gulf of Alaska between Cape Spencer and Yakutat Bay (outside waters, Figure 1) and 34 sites in protected waters between northern Lynn Canal and Frederick Sound (inside waters, Figure 2). Each site was sampled once.

Pacific cod were caught with traps (360 fish) and gill nets (160 fish) in water 38-176 m deep (Table 1). Most fish were caught in waters <90 m deep. Traps, 0.8×0.8×2.4 m rectangular structures with tunnel openings, were baited with chopped frozen Pacific herring, *Clupea harengus pallasi*, and set on the bottom. Gill nets, 180 m long, made of 15 cm or 17.5 cm diagonal-stretched-mesh monofilament, were set on the bottom or 0.6 m above the bottom. Both gear were set during daylight hours, fished overnight, and retrieved the

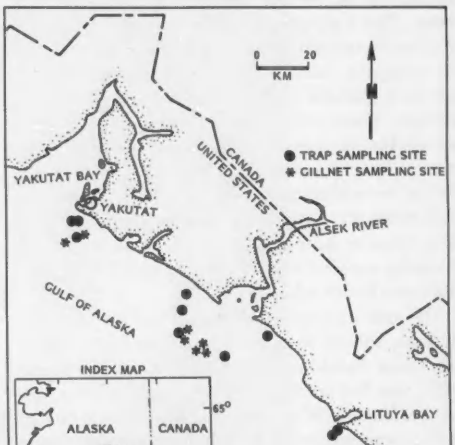

FIGURE 1.—Locations where Pacific cod were sampled in outside waters, southeastern Alaska, July 1977.

[1]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948-1976 (a historical review). Processed rep., 955 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[2]North Pacific Fishery Management Council. 1978. Fishery management plan for the Gulf of Alaska groundfish fishery during 1978. Unpubl. rep., 220 p. North Pacific Management Council, P.O. Box 3136DT, Anchorage, AK 99510.

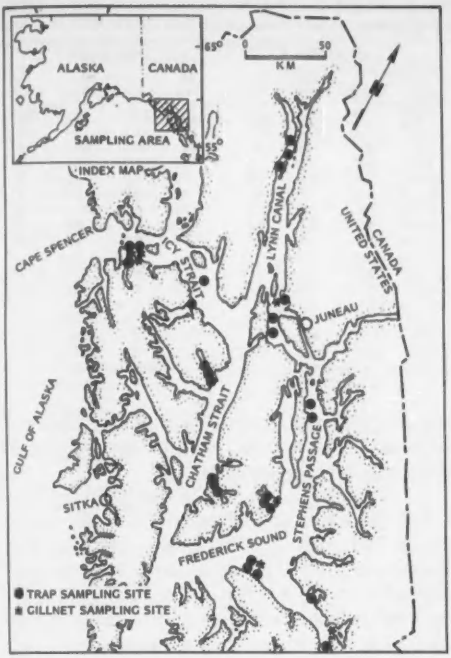

FIGURE 2.—Locations where Pacific cod were sampled in inside waters, southeastern Alaska, July 1977.

TABLE 1.—Summary of samples of Pacific cod caught in gill nets and traps in southeastern Alaskan waters, July 1977. Each site was sampled once.

	Caught in gill nets				Caught in traps			
Area	Sites (no.)	Mean depth (m)	Cod (no.)	Mean length (cm)	Sites (no.)	Mean depth (m)	Cod (no.)	Mean length (cm)
Outside waters	7	149	81	73.9	10	63	135	60.7
Inside waters	7	52	79	72.7	27	70	225	66.0
Both	14	101	160	73.3	37	68	360	64.0

next day. Usually, stomachs were removed from all Pacific cod caught, but random subsamples were taken from a few large catches. Stomachs and regurgitated or undigested food in the esophageal and mouth areas were preserved in Formalin.[3] The sex of each Pacific cod was identified, if possible, and the total length (TL, tip of snout to end of tail) was measured.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Estimated percentage volume of major food categories and frequency of occurrence of each food were determined. The volume of each major food category (i.e., fish, pandalid shrimp) was visually estimated to the nearest 5% for each stomach that arbitrarily appeared to be at least one-fourth full. Foods in stomachs less than one-fourth full were listed only as present and often were slowly digested items, such as fish otoliths or cephalopod beaks in trace amounts. No other allowances were made for stomach fullness. When pooling results, I averaged equally the percentages of each food in all stomachs one-fourth or more full. Visual estimates of the percentage volume of food in each category were generally within 10% of percentages determined by actual measurements of displacement volume. I identified all foods in all stomachs to the lowest taxonomic level possible and calculated the overall frequency of occurrence (expressed as the percentage of stomachs containing the food) of each food.

Volume data on each major food category were analyzed to determine whether relationships existed between foods eaten by Pacific cod and 1) size and sex of Pacific cod, 2) the location at which they were caught (inside waters vs. outside waters), and 3) the type of gear. I arbitrarily separated the Pacific cod into three total length categories to determine whether the different foods eaten were related to size of Pacific cod. The size categories were ≤60 cm, 61-70 cm, and >70 cm. Too few samples were taken at different depths in the same localities to allow analysis of Pacific cod foods by depth.

Results

If data from all areas are combined, regardless of size and sex of Pacific cod and gear type, fish were the most important food of Pacific cod both volumetrically and in frequency of occurrence. Fish accounted for more than 40% of the stomach contents by volume (Table 2) and were in nearly 60% of the stomachs (Table 3). The largest percentage of fish in the stomachs was unidentifiable; however, of the identifiable fish, Pacific herring and walleye pollock, *Theragra chalcogramma*, were eaten most often. Pacific herring ranged from 9 to 25 cm long (mean, 18 cm); walleye pollock, identified by their large and characteristic otoliths, were juveniles and ranged from 10 to 31 cm long (mean, 22 cm). Some of the unidentified fish were probably Pacific herring, pricklebacks

TABLE 2.—Mean estimated percentage volume of foods in stomachs of Pacific cod in southeastern Alaskan waters, July 1977 (stomach fullness one-fourth or greater).

	All areas						Outside waters				Inside waters			
Food item	All fish	All males	All females	≤60 cm	61-70 cm	>70 cm	All fish	≤60 cm	61-70 cm	>70 cm	All fish	≤60 cm	61-70 cm	>70 cm
Fish	42.5	39.4	44.9	17.1	35.4	66.0	35.1	11.9	27.8	61.9	48.0	22.7	40.5	68.7
Crab	26.1	26.5	25.2	38.0	30.3	14.3	44.9	57.7	56.7	21.1	12.1	16.3	12.4	9.8
Shrimp	16.9	21.8	13.9	23.0	20.3	9.1	4.7	6.3	5.0	2.7	26.1	41.6	30.7	13.4
Pandalid	9.7	14.2	7.3	5.6	13.7	7.1	1.0	1.7	.5	.9	16.2	9.9	22.7	11.2
Crangonid	3.5	3.4	3.4	9.6	2.6	1.1	2.6	3.5	2.7	1.5	4.3	16.3	2.6	.9
Hippolytid	2.3	2.9	2.0	4.9	2.5	.6	.3	1.1	.1	0	3.8	9.2	4.0	.9
Unidentified	1.4	1.3	1.2	2.9	1.5	.3	.8	0	1.7	.3	1.8	6.2	1.4	.4
Gammarid amphipods	3.5	4.3	3.0	6.9	3.8	1.1	3.8	8.7	2.1	2.3	3.2	4.9	5.0	.2
Cephalopods	3.1	2.2	3.9	2.8	3.6	2.9	1.0	2.9	.5	.2	4.7	2.8	5.6	4.6
Molluscs other than cephalopods	1.7	1.2	1.9	2.7	1.8	1.0	.9	.7	1.5	.9	2.3	4.8	2.0	1.2
Polychaetes	2.2	1.1	2.9	3.0	2.3	1.7	4.2	5.0	3.6	4.3	.7	.8	1.4	0
Other food items and unidentified	4.0	3.5	4.3	6.5	2.5	3.9	5.4	6.8	2.8	6.6	2.9	6.1	2.4	2.1
Cod sampled (no.)	439	163	266	90	193	156	187	47	78	62	252	43	115	94
Mean total length (cm)	67.0	65.2	68.6	53.7	65.6	77.0	65.7	52.2	65.4	77.6	67.7	55.4	65.8	76.6

(Stichaeidae), and eelpouts (Zoarcidae), which are not as distinguishable as walleye pollock and may have been eaten more frequently than the values in Table 3 indicate. Flatfish (Pleuronectidae) were easily recognized and, because few were found, were probably not an important food for Pacific cod in these waters during July.

Crab and shrimp were the next most important foods. The volume of crab in Pacific cod stomachs was greater than the volume of shrimp; however, the frequency of occurrence of shrimp was greater than the frequency of occurrence of crab. Snow crab, *Chionoecetes bairdi*, the crab most often eaten by Pacific cod, were juveniles and ranged from 5 to 42 mm carapace width (mean, 20 mm). As many as 30 snow crabs were found in some stomachs. Dungeness crab, *Cancer magister*, was the only other crab eaten in more than incidental numbers. Pagurids (hermit) and other anomuran crabs were rarely eaten. Pandalid shrimp, particularly *Pandalus tridens* and *P. borealis*, were more frequently eaten than either crangonid or hippolytid shrimp, and all three families of shrimp were often found together in stomachs.

Other invertebrates were found in the Pacific cod stomachs, but their volumes and frequencies were small. Cephalopods were in more than 14% of the stomachs but constituted only 3.1% of the mean volume. Often only the cephalopod's horny beaks were present; however, whole *Octopus* sp. formed the bulk of the stomach contents of a few Pacific cod. Gammarid amphipods were in 14% of the stomachs. Pelecypods, mostly *Nuculana* sp., were infrequently eaten. The large polychaete *Aphrodita* sp. ("sea mouse") was found in some stomachs and composed most of the volume for the polychaetes. Planktonic foods, such as euphausiids or mysids, were rarely found and then, only in trace amounts.

At all locations, the size of the Pacific cod affected the kinds of food eaten (Table 2). Small Pacific cod (≤60 cm) fed mostly on crab and shrimp; only 17% of the estimated volume of their stomach contents was fish. Large Pacific cod (>70 cm long) fed predominately on fish (66% by volume). The diet of intermediate-sized Pacific cod (61-70 cm) was transitional between the diets of the small and large Pacific cod.

Sex of Pacific cod did not appear to be related to the major foods eaten (Table 2). Fifty-nine percent of the Pacific cod were females, 38.7% were males, and 2.3% were of unidentified sex. Females had a mean of 68.6 cm TL; males, 65.2 cm TL. The minor differences that did arise between the foods of each sex can probably be attributed to the greater mean length of females.

Foods of Pacific cod in outside waters were different from foods of those in inside waters (Tables 2, 3). Pacific cod in outside waters ate a larger volume of crabs (mostly juvenile snow crab) than those in inside waters; however, in inside waters, the volume of shrimp (particularly pandalid shrimp) in the stomachs was much higher than in outside waters. These differences in the volume of foods eaten were especially pronounced for small and intermediate-sized Pacific cod. All sizes of Pacific cod ate more fish in the inside waters than in the outside waters. Pacific herring, especially, were heavily consumed in inside waters.

The two gear (gill nets and traps) probably did not significantly bias the results. Comparison of foods in Pacific cod caught by gill nets and foods in

TABLE 3.—Frequency of occurrence of food items ≥1.0% in stomachs of 492 Pacific cod, southeastern Alaskan waters, July 1977 (based only on stomachs containing food).[1]

Food item	Frequency of occurrence (%)		
	All areas	Outside waters	Inside waters
Fishes	58.5	54.2	61.5
Clupea harengus pallasi	9.6	1.0	15.5
Theragra chalcogramma	8.7	8.5	8.9
Stichaeidae	2.8	.5	4.5
Unidentified stichaeids	2.2	.5	3.4
Pleuronectidae	1.8	2.5	1.4
Unidentified pleuronectids	1.0	.5	1.4
Zoarcidae	1.2	.5	1.4
Unidentified	36.4	38.3	35.1
Shrimps	46.5	24.9	61.5
Pandalidae	25.4	7.0	38.1
Pandalus tridens	5.5	4.5	6.2
P. borealis	4.7	0	7.9
P. danae	1.8	0	3.1
P. hypsinotus	1.6	0	2.7
Unidentified pandalids	15.2	1.7	24.1
Crangonidae	18.9	16.9	20.3
Crangon spp.	8.9	6.0	10.7
Argis sp.	1.0	2.0	.3
Unidentified crangonids	9.2	9.0	8.6
Hippolytidae	9.6	1.5	15.1
Unidentified shrimp	7.7	4.5	10.0
Crabs	39.6	62.7	23.7
Brachyuran crabs	32.3	58.2	14.4
Chionoecetes bairdi	26.2	44.8	13.4
Cancer magister	4.1	10.0	0
Hyas lyratus	1.0	1.5	.7
Unidentified brachyurans	2.2	4.0	1.0
Anomuran crabs	3.7	1.0	5.5
Unidentified pagurids	2.8	.5	4.5
Unidentified crabs	2.6	2.5	2.7
Cephalopods	14.4	9.5	17.9
Octopus sp.	4.1	1.5	5.8
Unidentified cephalopods	10.0	7.0	12.0
Gammarid amphipods	14.0	16.4	12.4
Pelecypods	11.4	7.5	14.1
Nuculana sp.	7.5	3.0	10.7
Unidentified pelecypods	3.3	3.0	3.4
Polychaetes	6.5	10.9	3.4
Aphrodita sp.	3.7	8.5	.3
Unidentified polychaetes	2.6	2.5	2.7
Gastropods	3.9	2.5	4.8
Natica sp.	1.2	2.0	.7
Unidentified gastropods	2.2	0	3.8
Algae	3.0	3.0	3.1
Euphausiids	3.0	0	5.1
Isopods	1.6	2.5	.3
Rocinela sp.	1.6	2.5	.3
Mysids	1.0	0	1.7
Unidentified food items	2.6	3.5	2.1

[1]Also present at frequencies <1.0%: Fishes—*Lumpenus maculatus*, *L. sagitta*, *Hippoglossoides elassodon*, *Lepidopsetta bilineata*, *Lycodes brevipes*, *L. palaeris*, *Dasycottus setiger*, *Coryphaenoides* sp., *Raja* sp. embryo, unidentified fish eggs; shrimps—*Pandalus stenolepis*, *P. goniurus*, *P. platyceros*; crabs—*Oregonia gracilis*, *Lopholithodes* sp., *Labidochirus splendescens*; cephalopods—*Rossia pacifica*; pelecypods—*Siliqua patula*, *Chlamys rubidus*, *Serripes groenlandicus*; polychaetes—*Abarenicola* sp.; gastropods—*Lora* sp., *Neptunea* sp.; barnacles—*Lepas* sp., unidentified barnacles; sipunculids; hydroids; ophiuroids; nemerteans; anthozoans; poriferans; foraminifera; unidentified invertebrate eggs.

Pacific cod caught by traps was difficult because the two gear, which tend to catch different sizes of fish, were frequently set at different localities or depths (Table 1; Figures 1, 2). However, when traps and gill nets caught similar-sized fish in the same areas, foods were also similar (see Table 4, Pacific cod 61-70 cm TL in outside waters and >70 cm TL in inside waters). In other cases, locality rather than gear appeared to be the overriding factor determining kinds of food eaten. Of the 24 Pacific cod sampled in the 61-70 cm TL gill net category in inside waters, 15 were taken in Idaho Inlet. There, Pacific herring apparently were so abundant that all sizes of Pacific cod caught in both gill nets and traps fed upon them.

The volume of gammarid amphipods in the stomachs of Pacific cod caught in traps may have been artificially high. Gammarid amphipods were almost exclusively found in Pacific cod caught in traps (Table 4). These amphipods were probably attracted to the baited traps where Pacific cod in the traps fed upon them. In contrast, other invertebrates, such as shrimp or crabs, appeared to be found equally in stomachs of Pacific cod caught in either traps or gill nets.

Discussion

The major foods identified in this study are similar to the major foods of Pacific cod in other regions of the North Pacific Ocean. Walleye pollock and Pacific herring were among the predominate fish species in stomachs of Pacific cod from Asian waters, and the crab *Chionoecetes* sp. was the most common invertebrate (Moiseev 1953). Flatfish and the sand lance, *Ammodytes* sp., however, appeared frequently in Moiseev's samples of Pacific cod stomachs but were rare or absent in my samples. The results of Jewett's (1978) study are in close agreement with the results of my study: he found fish, crab, and shrimp to be the most frequent items in Pacific cod stomachs collected near Kodiak, Alaska, during summer. In Jewett's study, walleye pollock was the most common fish eaten, and snow crab was the most common crab; Pacific herring were rarely eaten.

Other studies have demonstrated, as did my study, that larger codfishes become more piscivorous. As the size of Atlantic cod, *Gadus morhua*, increased, the diet changed from smaller invertebrates to larger fish (Powles 1958; Popova 1962; Rae 1967). Both Moiseev (1953) and Jewett (1978) found similar trends in their investigations of Pacific cod: cod <50-60 cm long ate mostly crustaceans; cod >60 cm primarily ate fish.

Some of the differences I found in foods of Pacific cod in outside and inside waters may be related to the availability of pandalid shrimp and Pacific herring. The results of my food study appear to reflect an increased abundance of both of these two foods in inside waters. Data from exploratory

TABLE 4.—Mean estimated percentage volume of food in stomachs of Pacific cod, by total length of cod and gear type, southeastern Alaskan waters, July 1977 (stomachs one-fourth full or greater).

	Outside waters						Inside waters					
	≤60 cm		61-70 cm		>70 cm		≤60 cm		61-70 cm		>70 cm	
Item	Nets	Traps	Nets	Traps	Nets	Traps	Nets	Traps	Nets	Traps	Nets	Traps
Fish	80.0	10.4	31.0	26.2	69.8	37.4	68.3	19.3	67.2	33.5	74.2	63.3
Crab	0	56.8	54.2	57.8	12.4	48.3	1.7	17.5	5.2	14.5	7.9	11.8
Shrimp	10.0	6.4	8.2	3.6	2.4	3.7	30.0	42.4	17.7	33.9	11.1	15.7
Pandalid	0	1.7	.6	.5	.4	2.4	30.0	8.4	16.2	24.2	8.0	14.5
Crangonid	10.0	3.6	3.0	2.6	1.6	1.3	0	17.5	1.5	2.9	1.5	.2
Hippolytid	0	1.1	.2	0	0	0	0	9.9	0	5.1	1.3	.6
Unidentified	0	0	4.4	.5	.4	0	0	6.6	0	1.7	.3	.4
Gammarid amphipods	5.0	8.8	.6	2.8	0	9.7	0	5.2	0	6.4	0	1.5
Mollusks												
Cephalopods	0	2.9	1.0	.3	.2	.3	0	3.0	9.6	4.5	4.6	3.5
Other mollusks	0	.5	0	1.7	.7	.3	0	6.0	.3	2.3	1.3	.9
Polychaetes	0	5.1	3.4	3.8	5.5	.3	0	0	0	2.0	.1	0
Other foods and unidentified	5.0	6.8	1.6	3.8	9.0	0	0	6.6	0	2.9	.8	3.3
Cod caught (no.)	1	46	25	53	47	15	3	40	24	91	47	47
Mean total length (cm)	44.0	52.4	65.4	65.4	78.8	73.7	58.3	55.2	66.9	65.5	76.4	76.7

trawling surveys indicate pandalid shrimp are very low in abundance in outside waters (Schaefers and Smith 1954; Hitz and Rathjen 1965; Ronholt et al.[4]). From 1969 to 1975, no pandalid shrimp were commercially landed in this area (Ronholt et al. footnote 1). However, in the inside waters of southeastern Alaska around Petersburg, near the southern portion of my sample area, pandalid shrimp have been fished commercially since 1916 (Barr 1970). In northern inside waters, pandalid shrimp have also been reported as abundant (Ellson and Livingstone 1952). Similarly, since commercial fishing records were first kept in the 1920's, Pacific herring have been abundant in inside waters south of Cape Spencer (Reid 1971). No catches of Pacific herring have ever been reported for outside waters north of Cape Spencer apparently because of the scarcity of Pacific herring in this area.

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[4]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1976. An assessment of the demersal fish and invertebrate resources of the northeastern Gulf of Alaska. Yakutat Bay to Cape Cleare, May-August 1975. NEGOA Annual Report, 183 p. Processed rep. Northwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

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USE OF GRIFFIN'S YIELD MODEL FOR THE GULF OF MEXICO SHRIMP FISHERY[1]

For analyzing the harvest of the Gulf of Mexico shrimp fishery, Griffin et al. (1976) have developed an equation that relates shrimp yield to freshwater discharge of the Mississippi River and fishing effort of Gulf shrimp vessels. The yield equation (referred to as Griffin's equation) is a modified Spillman production function (Heady and Dillon 1972). The Spillman function had its origin in agriculture where it was derived to predict the results of fertilizer experiments on tobacco yield in North Carolina. An important feature of the function is that it allows for environmental considerations in predicting yield. The modified form of the equation proposed by Griffin et al. (1976) is:

$$Y = \beta_0 D^{\beta_2} (1 - \beta_1^E) \qquad (1)$$

where Y = yield of shrimp (million pounds),[2]
D = average daily discharge of the Mississippi River during the months that shrimp are in their nursery grounds (cubic feet per second),
E = vessel effort (thousand units),
$\beta_0, \beta_1, \beta_2$ = parameters to be estimated from data of the fishery.

The coefficients of Equation (1) were estimated from individual vessel records collected by the National Marine Fisheries Service and from measurements of water flow rates on the Mississippi River for the years 1962-74. According to Griffin and Beattie (1978), the fit was quite good, namely: "All estimated coefficients were significant at the 1% level; R^2 was 78.5; and the Durbin-Watson statistic was 2.25. The simple correlation coefficient between catch and effort was 0.64 and between catch and discharge was −0.63."

Griffin's equation has found numerous uses in the Gulf shrimp management literature. Griffin and Beattie (1978) used the equation to estimate the impact of effort reallocation as a result of Mexican extended jurisdiction; the Gulf Coast Research Laboratory at Ocean Springs, Miss., (Christmas and Etzold 1977) used the equation for similar purposes; and the Center for Wetland Resources, Louisiana State University[3] used the equation to estimate maximum sustainable yield for management considerations.

Despite the extensive usage, users have not critically reviewed Griffin's equation. Such a review is necessary because of the large-scale potential impact of proposed shrimp management plans. In view of this need, therefore, I subjected Griffin's equation to such a review.

The review consisted of two tests relevant to the usage of Griffin's equation in management decisions. In the first test, I estimated the error in expected yield introduced by the typical user who ignored the fact that the independent variables—effort and river discharge—have variances. For convenience, this was termed the "expected value test." In the second test, I depicted the error in yield estimate that would result from misspecification of model parameter estimates. For convenience, this test was termed the "sensitivity test."

The results were mixed. The expected value test produced a large absolute error in expected yield of shrimp. However, when compared with expected yield, the error was proportionally small. The sensitivity test produced some startling results. Yield turned out to be very significantly sensitive to a fixed model parameter whose constancy was conceptually questionable in the first place. This extreme sensitivity of yield raises questions regarding the reliability of Griffin's equation as a shrimp management tool.

Each test is discussed below in detail.

[1]Contribution No. 80-54M, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, Fla.

[2]The original equation was estimated by Griffin et al. (1976) in nonmetric units and its nonlinear nature excludes conversion to metric units.

[3]Louisiana State University. 1979. Draft fishery management plan for shrimp fishery. Prepared by Center for Wetland Resources, L.S.U., Baton Rouge, 226 p.

Expected Value of Yield

Most users of Griffin's equation (Griffin et al. 1976; Louisiana State University (footnote 3) estimated yield by using the mean (or expected) value of the independent variables, discharge and effort. Yet it can easily be shown that, for a general two-variable function, if x, y are random variables and g an arbitrary twice differentiable function of x, y such that:

$$z = g(x,y) \tag{2}$$

then $$E[z] = E[g(x,y)] \neq g(E[x], E[y]) \tag{3}$$

or if $E[x] = \eta_x$ and $E[y]\ \eta_y$

then $$E[z] \neq g(\eta_x, \eta_y) \tag{4}$$

where $E(\cdot)$ denotes expectation of random variable.

Hence, yield estimates obtained using mean values as in Equation (4) are generally not accurate. It may be shown (Papoulis 1965) that Equation (4) may be correctly approximated as:

$$E[z] = g(\eta_x,\eta_y) + \frac{1}{2}\left\{\frac{\partial^2 g}{\partial x^2}\ \sigma_x^2 + \frac{\partial^2 g}{\partial y^2}\ \sigma_y^2 + \frac{2\partial^2 g}{\partial x \partial y}\ \mathrm{cov}\,(x,y)\right\} + \ldots \tag{5}$$

where the o^2's are the variances of variables x,y. The variance of the estimate is as follows:

$$\sigma_z^2 = \left\{\frac{\partial g}{\partial x}\right\}^2 \sigma_x^2 + \left\{\frac{\partial g}{\partial y}\right\}^2 \sigma_y^2 + 2\left\{\frac{\partial g}{\partial x}\ \frac{\partial g}{\partial y}\right\}\ \mathrm{cov}(x,y) + \ldots . \tag{6}$$

Thus, Equation (4) is only a first approximation, with Equation (5) providing the second term. Additional terms may be obtained by continuing Taylor's series expansion of $g(x,y)$ around $g(\eta_x, \eta_y)$. For the purpose of the test, however, the second term was sufficient.

For Griffin's equation the independent (random) variables were river discharge D and vessel effort E. So, the expected value of the dependent (random) variable yield Y could be expressed as:

$$E[Y] = Y(\eta_D,\eta_E) + \frac{1}{2}\left\{\frac{\partial^2 Y}{\partial D^2}\bigg|_{\eta_D}\ \sigma_D^2 + \frac{\partial^2 Y}{\partial E^2}\bigg|_{\eta_E}\ \sigma_D^2 + 2\frac{\partial^2 Y}{\partial D \partial E}\bigg|_{\eta_D,\eta_E}\ \mathrm{cov}\,(D,E)\right\}. \tag{7}$$

Similarly, the variance of the estimate was given by:

$$\sigma_y^2 = \left\{\frac{\partial Y}{\partial D}\right\}^2\bigg|_{\eta_D}\ \sigma_D^2 + \left\{\frac{\partial Y}{\partial E}\right\}^2\bigg|_{\eta_E}\ \sigma_E^2 + 2\left\{\frac{\partial Y}{\partial D}\cdot\frac{\partial Y}{\partial E}\right\}\bigg|_{\eta_D,\eta_E}\ \mathrm{cov}(D,E)\ . \tag{8}$$

To compute the estimated yield and its variance we required the first, second, and cross partial derivatives of the yield equation. The derivation was tedious and hence not reproduced here. By the necessary partial differentiation of Equation (1) we could write:

$$\frac{\partial Y}{\partial D} = \beta_2\beta_0 D^{\beta_2 - 1}\ (1 - \beta_1^E) \tag{9}$$

$$\frac{\partial^2 Y}{\partial D^2} = \beta_2\ (\beta_2 - 1)\ \beta_0 D^{\beta_2 - 2}\ (1 - \beta_1^E) \tag{10}$$

$$\frac{\partial Y}{\partial E} = -\beta_0 D^{\beta_2}\ \beta_1^E\ \log_e \beta_1 \tag{11}$$

$$\frac{\partial^2 Y}{\partial E^2} = -\beta_0 D^{\beta_2}\ \beta_1^E\ (\log_e \beta_1)^2 \tag{12}$$

$$\frac{\partial^2 Y}{\partial D \partial E} = -\beta_0\beta_2\ D^{\beta_2 - 1}\ \beta_1^E\ \log_e \beta_1\ . \tag{13}$$

Griffin et al. (1976) have estimated the equation parameters to be: $\beta_0 = 6593$, $\beta_1 = 0.995701$, and $\beta_2 = -0.60134$.

Expected yield of shrimp can be determined by using the means, variances, and covariances of river discharge and effort. Following the approach of one user of Griffin's equation (Christmas and Etzold 1977), yield was estimated by using mean values of variables for the years 1970-74. A listing of the data and numerical values of means and covariances are given in Table 1.

TABLE 1.—Data, including mean and variance of Mississippi River discharge (thousand cubic feet per second) at Tarbert Landing, Miss., and Gulf of Mexico commercial shrimp effort (thousands of days) from U.S. waters by vessel, 1970-74.[1]

	Discharge						
Year	Jan.	Feb.	Mar.	Apr.	May	Mean Jan.-May	Effort
1970	448	430	529	652	852	582.2	249.1
1971	482	481	865	449	431	541.6	259.0
1972	560	427	602	536	749	574.8	282.6
1973	842	857	779	1,284	1,373	1,027	269.7
1974	971	1,083	828	792	576	850.00	243.6
Averages				ηD =	715.1	ηE =	260.8
SD				σD =	213.9	σE =	15.74
Covariance				$\mu D, E$ =	−141.92		

[1]Sources: U.S. Army Corps of Engineers, Stages and discharges of the Mississippi River and its tributaries and other watersheds in New Orleans District. U.S. Army Engineer District, New Orleans Corps of Engineers, Louisiana, and Christmas and Etzold 1977:28).

Appropriate insertion of these numerical values in Equation (7) produced the following estimates of yield:

$$E(Y) = 89.09 \text{ million lb}, \sigma_y^2 = 247.72.$$

Ignoring the variances and covariances, as most users of Griffin's equation do, we computed the corresponding estimated yield to be: $E(Y) = 85.48$ million lb.

The expected value test indicated that an absolute error of 3.6 million lb of shrimp is introduced by ignoring the variances and covariances of the independent variables. While an error of 3.6 million lb is large in absolute terms, its significance is diminished to 4% in relative terms. Furthermore, although 4% error is sizable, it is probably insufficient to alter economic management conclusions. We may conclude, therefore, that the expected value test, if applied to other applications of Griffin's equation, would not drastically alter management conclusions.

Parameter Sensitivity Test

Griffin's equation contains three parameters, each with its own significance and sensitivity. (Absolute and relative definitions of sensitivity can be found in Tomovic and Vukobratovic (1972) and Truxal (1972).) In assessing the sensitivity of yield to these parameters, I will relate proportional changes in parameter values to proportional changes in yield. (For this application of the sensitivity test, the relative measure of sensitivity is preferred because the results obtained are independent of the units of measure used for effort and discharge.) Mathematically, the sensitivity S of yield to parameter β may be expressed as:

$$S(Y|\beta) \triangleq \frac{\partial(\log_e Y)}{\partial(\log_e \beta)} = \frac{\partial Y/Y}{\partial \beta/\beta} = \frac{\partial Y}{\partial \beta}\cdot\frac{\beta}{Y}. \quad (14)$$

In considering parameter β_0, note that it is the dimensioned constant relating effort, discharge, and yield. The sensitivity of yield to β_0 is expressed:

$$S(Y|\beta_0) = 1.0. \quad (15)$$

In Equation (15), the sensitivity is small and constant. Thus, small errors in misspecification of β_0 will not significantly affect yield estimates.

Parameter β_2 governs the relationship between discharge of the Mississippi River and yield. Its sensitivity can be expressed as:

$$S(Y|\beta_2) = \beta_2 \log_e D. \quad (16)$$

The relationship is clearly linear and the sensitivity relatively small (Figure 1). Again, the implication being that misspecification of β_2 or future changes in its value would have small impact on yield.

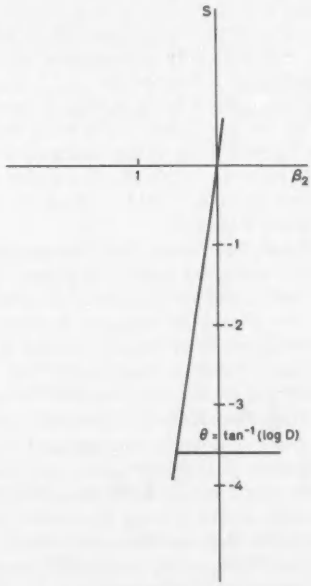

FIGURE 1.—Sensitivity (S) of yield to parameter β_2; i.e., the percentage change in yield corresponding to a 1% change in β_2.

The parameter β_1 is a little more difficult to understand. In the context of the model, β_1 is the constant that relates marginal yield corresponding to two successive units of effort. By appropriate manipulation of Equation (1) we can derive the following expression:

$$\beta_1 = \frac{\left.\frac{\partial Y}{\partial E}\right|_{\tilde{E}+1}}{\left.\frac{\partial Y}{\partial E}\right|_{\tilde{E}}}. \qquad (17)$$

Rational physical arguments may be used to show that β_1 is bounded by 0 and 1 ($0<\beta_1<1$). The law of diminishing returns provides the simplest argument, although there are others. Nevertheless, whatever the interpretation of β_1, sensitivity of yield to the parameter can be expressed as:

$$S(Y|\beta_1) = \frac{-E}{\beta_1^{-E}-1}. \qquad (18)$$

Since we have already established $0<\beta_1<1$, Equation (18) can be sketched as shown in Figure 2.

Yield is not very sensitive to β_1 for small values of $\beta_1 (\approx 0)$. The sensitivity increases hyperbolically, however, asymptotically approaching infinity as β_1 approaches the value unity.

Griffin's estimate of β_1 is 0.995701. This is about as close as one could get to the most sensitive region in Figure 2. For a value of effort E of 260.8, the sensitivity is −125.63. Thus any small misspecification of β_1 would produce very large errors in yield estimates.

It has already been shown that the parameter β_1 is related to marginal product of effort. At this point I question the assumption of β_1 as being a constant parameter. The marginal product of effort in any fishery is intimately related to stock and fleet characteristics. Realistically, one would expect marginal product and therefore its ratio to vary over time. Even if one could consider β_1 to be a constant over 1 yr, it would most certainly change over the course of the 12 yr that were used to estimate the given value (Griffin et al. 1976). Since I have already shown β_1 to be the most sensitive parameter of Griffin's equation, any misspecification or future change of β_1 would have enormous consequences on yield estimates.

Thus a user of Griffin's equation, who assumes a value of β_1 based on previous estimates of stock, effort, etc., may make incorrect predictions in the face of changing conditions. This observation severely limits the applicability of Griffin's equation for management purposes.

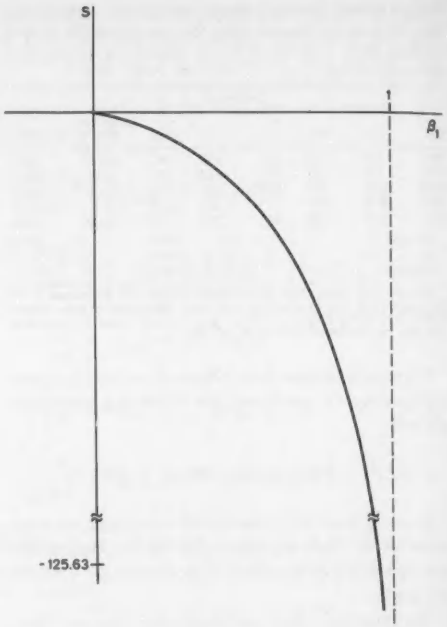

FIGURE 2.—Sensitivity (S) of yield to parameter β_1; i.e., the percentage change in yield corresponding to a 1% change in β_1.

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SEASONAL SPAWNING CYCLE OF THE PACIFIC BUTTERFISH, *PEPRILUS SIMILLIMUS* (STROMATEIDAE)

There is little information on the reproductive biology of the Pacific butterfish, *Peprilus simillimus*, which ranges from Magdalena Bay, Baja California, to the Fraser River, British Columbia, and occurs at depths of 9-91 m (Miller and Lea 1972). It is commercially fished with purse seine, lampera, and bait net (Fitch and Lavenberg 1971). In 1976, 34.18 t were taken in California (Oliphant 1979). Fitch and Lavenberg (1971) reported spawning occurs in spring and extends perhaps into July. Horn (1970) studied the systematics and biology of the genus *Peprilus*. My purpose is to describe histologically the seasonal spawning cycle of the Pacific butterfish.

Methods

Fish were collected with the use of a lampera net between depths of 2 and 20 m from the vicinity of Oceanside, southern California (lat. 33°10′ N, long. 117°25′ W), during the period September 1978 through August 1979. Only female specimens were examined. Fish were fixed and preserved in 10% Formalin.[1] Ovarian histological sections from 232 specimens were cut at 8 μm and stained with iron hematoxylin. Seasonal gonosomatic indices (ovary weight/fish weight × 100) were calculated from preserved fish. Ovaries were histologically classified into four stages (Table 1).

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Monthly distribution (percent) of ovarian stages in the yearly spawning cycle of *Peprilus simillimus*, September 1978-August 1979.

Month	N	Regressed or regressing	Pre-vitellogenic	Vitellogenic	Pre-spawning
Sept.	25	100	0	0	0
Oct.	18	100	0	0	0
Nov.	15	100	0	0	0
Dec.	17	53	47	0	0
Jan.	21	52	43	5	0
Feb.	19	26	42	16	16
Mar.	20	10	15	0	75
Apr.	20	5	5	0	90
May	16	44	19	0	37
June	20	95	0	0	5
July	17	100	0	0	0
Aug.	24	92	8	0	0

Results

Ovaries were regressed (Stage 1) during autumn (September-November) and consisted of primary oocytes <100 μm in diameter (Table 1). Gonosomatic indices (Figure 1) were reduced at this time. The first signs of ovarian activity for the new spawning cycle were noted during December. This was determined by an abundance of previtellogenic (vacuolated) (Stage 2) oocytes (130-200 μm) which typically appear before yolk deposition begins (Table 1). Enlarging (Stage 3) vitellogenic oocytes (yolk deposition in progress) were first noted in January. The first ripe (prespawning or gravid) (Stage 4) females with ovaries containing

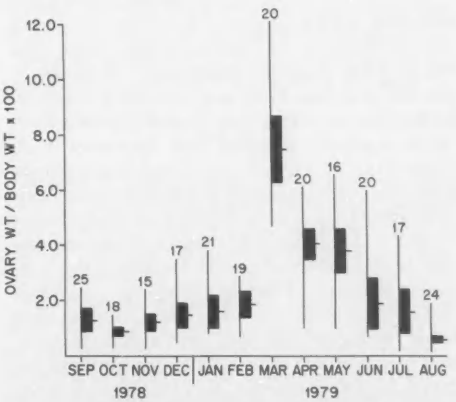

FIGURE 1.—Seasonal gonosomatic indices for *Peprilus simillimus*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval. Sample size above each month.

mature yolk-filled oocytes (>400 μm) were collected in February. Since only a small fraction of my February sample was gravid, the spawning period for the majority of the population under study appeared to encompass March-May (Table 1). The smallest reproductively active female measured 114 mm standard length (SL); the largest 172 mm SL. Gonosomatic indices were at maximum sizes in March (Figure 1) and a progressive decrease was indicated through spring with minimal sizes occurring by June. A May increase in the incidences of follicular atresia indicated the end of spawning was near. Atretic oocytes are most abundant near the termination of spawning when oocytes that initiated but failed to complete yolk deposition degenerate.

My observation of follicles in various stages of yolk deposition during the spawning period suggests that successive batches of eggs are matured and spawned. The number of spawnings per individual per season are not known, but the presence of a mode of mature oocytes (imminent spawning), postovulatory follicles (transitory remnant of the follicle wall from a recent spawning), and a vitellogenic oocyte mode for a subsequent spawning indicates that females are capable of spawning more than once per season. Postovulatory follicles were similar in morphology to those reported in other teleosts (Hunter and Goldberg 1980).

Discussion

Peprilus simillimus undergoes a distinctly seasonal spawning cycle characterized by an abrupt increase in ovarian sizes during late winter with spawning essentially completed by the end of spring. Fitch and Lavenberg (1971) reported that spawning may extend into July. Horn (1970) similarly reported that spawning in *P. triacanthus*, *P. burti*, *P. paru*, and *P. simillimus* generally occurs in spring and early summer. This contracted type of cycle differs from that of some southern California fishes that have a considerably longer spawning period. Goldberg (1980) reported that gravid female *Chitonotus pugetensis* and *Icelinus quadriceriatus* (both Cottidae) were found throughout the year with maximum numbers in winter and early spring. The northern anchovy, *Engraulis mordax*, may have the ability to spawn all year but is likely limited by food availability and energy reserves (Brewer 1978; Hunter and Goldberg 1980).

The *P. simillimus* spawning cycle is more reminiscent of northern fishes (Quasim 1956), which have a short reproductive period (generally winter-early spring) with a single spawning. The multiple spawnings over a brief period exhibited by *P. simillimus* may represent a compromise between a short reproductive period with a single spawning (characteristic of high latitude fishes) and a long reproductive period with repeated spawnings typical of tropical fishes (Nikolsky 1963).

Acknowledgments

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EFFECTS OF INJURIES ON SPINY LOBSTER, *PANULIRUS ARGUS*, AND IMPLICATIONS FOR FISHERY MANAGEMENT

The spiny lobster, *Panulirus argus*, supports important commercial and recreational fisheries throughout its range from Bermuda to Brazil. Its ecology and physiology are typical of a number of other commercially important palinurid species, which collectively have pantropic distributions (Phillips and Cobb 1977).

A variety of decapod crustacean responses to injuries, primarily limb loss, have been recorded. Aiken (1977) summarized a number of studies conducted in laboratories, some of which found that limb loss greatly accelerated ecdysis. Other observers noted limb loss resulted in reduced growth rates (Chittleborough 1975; Ford 1977; Savage and Sullivan 1978). This paper reports the effects of injuries on growth rates of wild juvenile spiny lobsters, *P. argus*, in Florida and discusses the implications of these effects on *P. argus* biology and its fishery.

Spiny lobsters (Palinuridae) have complex life cycles. Larval, early juvenile, and adult stages of the spiny lobster in Florida, *P. argus*, are ecologically dissimilar and are found separately in relatively discrete habitats. The planktonic phyllosoma larvae spend 5 to 9 mo in the open ocean before metamorphosing into actively swimming postlarvae, called pueruli (Lewis 1951). Pueruli swim into shallow coastal waters where they settle onto the bottom, assuming the benthic existence they will follow the rest of their lives. Postlarval and small juvenile spiny lobsters are found scattered throughout seagrass beds, particularly in shallow inshore areas like Biscayne Bay. Larger juveniles concentrate around rocky outcrops, sponges, and groups of sea urchins for shelter during the day (Khandker 1964; Davis 1971; Berrill 1975). They forage nightly on adjacent grassbeds and open sand areas for small mollusks, echinoids, and crustaceans (Herrnkind et al. 1975). Mature lobsters are generally associated with coral reefs, or other hard bottom, offshore to depths >150 m. The transition from inshore juvenile habitat to habitat offshore is sometimes accomplished by spectacular mass migrations, marked by long queues of lobsters (Herrnkind and Cummings 1964; Kanciruk and Herrnkind 1978).

The fishing season for *P. argus* in Florida extends slightly more than 8 mo from late July through March, with a special 2-d sport fishing season 5 d prior to the beginning of the regular sport and commercial season (Florida Statute 370.14). Recreational diving activity directed at spiny lobster harvest is particularly intense in nearshore areas during the first 6 to 8 wk of each season (Austin 1976). There are also over 1,000 commercial trappers, fishing up to 2,000 traps each, in the fishery (Beardsley et al. 1975).

Methods

At weekly or monthly intervals during 1976 and 1977, spiny lobsters were captured in southern Biscayne Bay, Fla., by hand, bully net, or tail snare and marked with spaghetti tags. The details and efficacy of this tagging procedure were reported by Davis (1978). Data on size (as carapace length, CL), injuries, molt condition, location, and water temperature were recorded. Injuries were recorded as the number of missing legs or antennae, or damage to the abdomen, cephalothorax, or supraorbital horns.

Growth of spiny lobsters takes place as the result of a series of molts, during which discontinuous size changes occur. The rate of growth is dependent on both magnitude of change in size with each molt (molt increment) and the length of the intermolt period. In this study, growth rate was expressed as change in carapace length per week, since nearly all observations of marked lobsters were made at weekly intervals. To reduce the variability inherent in measuring discontinuous changes in carapace length that resulted from random observations of growth during the molting cycle, all changes in size were summed over each class of observations (i.e., winter, summer, injured, or uninjured) and expressed as rates per week.

Results

A total of 7,643 *P. argus* were examined from February 1976 to December 1977. They ranged from 15 to 101 mm CL, with a mean of 60.7 mm CL (Table 1). Mean monthly water temperatures varied from 16° to 32° C.

Observations of growth were made for 844 time intervals, ranging from 1 to 82 wk (mean 20 wk), on 534 individual lobsters in the wild, ranging from 38 to 83 mm CL. Carapace length measurements were replicated by independent observers on the same day for 153 lobsters during the 22-mo tagging period to evaluate the precision of the carapace length measurements by various

TABLE 1.—Monthly summary of size, molting activity, and condition of spiny lobsters, and water temperatures in eastern Biscayne Bay, Fla., 1976-77.

Month	Number of lobsters	Size (mm CL)			Percentage		Mean water temp (°C)
		Min	Max	Mean	Molting	Injured	
1976:							
Feb.	1,247	34	84	56.1	8	53	16
Mar.	353	33	83	56.4	9	51	26
Apr.	464	38	86	60.0	12	45	25
May	362	34	79	59.4	12	39	27
June	340	43	87	63.2	14	46	29
July	414	15	85	61.6	8	31	31
Aug.	396	37	83	63.5	7	38	31
Sept.	217	40	96	63.1	6	42	30
Oct.	25	35	89	64.6	12	24	26
Dec.	139	38	85	54.7	13	42	17
1977:							
Jan.	86	33	85	57.7	43	37	16
Feb.	619	30	81	55.5	11	50	18
Mar.	387	31	88	57.3	7	49	23
Apr.	272	39	80	59.2	12	47	25
May	220	39	101	61.8	17	40	26
June	268	27	85	63.6	26	41	28
July	322	35	86	62.1	8	35	32
Aug.	414	30	84	63.6	17	31	32
Sept.	454	30	97	66.9	11	29	30
Oct.	335	32	99	65.3	13	35	27
Nov.	307	32	92	60.1	2	41	24
Total	7,643						
Mean		33.6	87.4	60.7	12.8	40.3	25.7

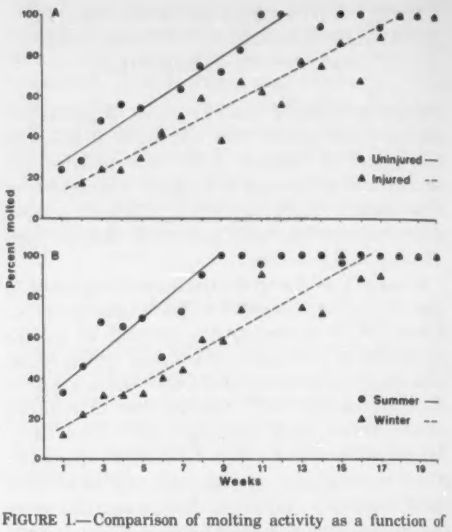

FIGURE 1.—Comparison of molting activity as a function of condition (A) and season (B) for spiny lobsters in Biscayne Bay, Fla.

technicians. The mean error was 0.3 mm, with a range of −1.8 to +2.1 mm. Consequently, only changes in carapace measurements >2.0 mm were recorded as growth, others were considered measurement errors.

Two factors appeared to affect growth rates: water temperature and lobster condition. Growth rate did not vary with either sex or size within the range observed. Mean intermolt periods were estimated by doubling the time interval over which 50% of the lobsters observed had molted. This assumed that at the time of tagging the lobsters were randomly distributed throughout their molting cycle (Munro 1974). This appeared reasonable since we observed molting activity throughout the year (Table 1), and direct observations of individual lobsters through periodic recaptures confirmed the mean values obtained for the population in this manner (Davis 1978). For example, during winter, the percentage of tagged lobsters that had molted increased weekly from 12% after 1 wk to 22, 31, 32, 40, 44, and 58% after 8 wk, indicating that 50% had molted after about 7.5 wk, resulting in a mean intermolt period of 15 wk (Figure 1). In contrast, the mean intermolt period during summer was only 8 wk (Table 2). The mean intermolt period of injured lobsters was 15 wk, and for uninjured lobsters it was 10 wk (Table 2). The mean growth increments were estimated by examining frequency distributions of observed changes in carapace length. Mean single molt growth increments were significantly larger during the summer and for uninjured lobsters than during the winter and for injured lobsters, respectively (Table 3). Effects of season and lobster condition on growth rate were independent (Table 4).

TABLE 2.—Mean growth variables determined from 1,688 observations on 534 tagged juvenile spiny lobsters in Biscayne Bay, Fla., 1976-1977.

Item	Number of growth intervals observed	Intermolt period (wk)	Observed growth rate (mm CL/wk)	Water temp (°C)
Season:				
Winter	656	15	0.31	21.1
Summer	146	8	0.75	29.1
Condition:				
Injured	465	15	0.31	[1]
Uninjured	379	10	0.51	[1]
All observations	844	12	0.41	25.7

[1]Not available.

Predictably, higher summer (May-October) temperatures and longer daylight periods were related to a greater growth rate (0.75 mm CL/wk) than that observed during winter, November through April (0.31 mm CL/wk). This 59% decrease in growth rate between summer and winter was apparently related to the 8.0° C decrease in mean water temperature, from 29.1° to 21.1° C, and the increased frequency of injuries incurred dur-

TABLE 3.—Comparison of mean molt increments (millimeters of change in carapace length) of juvenile spiny lobsters, in Biscayne Bay, Fla.

Item	Season		Conditions	
	Summer	Winter	Injured	Uninjured
$\bar{x}$	6.0	4.7	4.7	5.2
$S\bar{x}$	3.2	3.6	3.8	3.8
t, 306 df	7.75**		2.25*	

**$P \leq 0.01$; *$P \leq 0.05$.

TABLE 4.—Two-way fixed factor ANOVA of effects of season and spiny lobster condition as evidenced by growth rate.

Source of variation	df	SS	MS	F
Subgroups	3	106.50	35.50	
A (columns; condition)	1	34.60	34.60	4.65*
B (rows; season)	1	68.67	68.67	9.23**
A × B (interaction)	1	3.23	3.23	0.43n.s.
Within subgroups (error)	3,784	28,249.73	7.44	
Total	3,787	28,356.23		

*$P \leq 0.05$; **$P \leq 0.01$.

ing the fall and winter fishing season. Growth rates were lowest for injured lobsters during winter and highest for uninjured animals during summer, but injured lobsters grew faster in summer than injured ones in winter. Both of these factors, reduced temperature and injuries, caused increased intermolt periods and reduced molt increments, which resulted in reduced growth rates (Table 2). Change in the length of the intermolt period was the major effect of both factors, but by inspection of the values in Tables 2 and 3, it was apparent that intermolt period was proportionately more important for the injury-caused reduction, whereas decreased molt increment was proportionately more important for the season-related growth reduction.

Discussion

The growth data presented here generally conform both in magnitude and character to that in the published literature for decapod crustaceans, but the precise effect of injuries in the wild and definition of their origin is apparently new information, particularly for *P. argus*. Estimated growth rates for juvenile *P. argus* in the Caribbean, Florida, and Bermuda, range from 0.43 to 0.65 mm CL/wk (Smith 1951; Travis 1954; Sutcliffe 1957; Buesa M. 1965; Witham et al. 1968; Sweat 1968; Little 1972; Eldred et al. 1972; Ting 1973; Munro 1974; Peacock 1974; Olsen and Koblic 1975). The estimates for Biscayne Bay from this study ranged from 0.31 to 0.75 mm CL/wk, but the mean of 0.41 mm CL/wk was the lowest reported. The 1977 winter in Biscayne Bay was the coldest in the previous century (Molinari et al. 1977; McGuirk 1978), and the Bay is already near the northern limit of *P. argus* distribution. That cold winter depressed the mean growth rate somewhat, but another significant factor was that the Biscayne Bay lobster population was the most heavily fished by sport divers of all of those for which growth rates were reported. The injuries resulting from diver activity also depressed the growth rate. It appeared that a combination of cold weather and extremely high fishing activity caused the low growth rate reported in this study.

Variations in growth rates of lobsters have been attributed to several factors, the most common of which is temperature (Crawford and De Smidt 1922; Newman and Pollock 1974; Phillips et al. 1977). Limited food (Sutcliffe 1957; Chittleborough 1970; Newman and Pollock 1974), shelter (Chittleborough 1970), salinity and light (Travis 1954), and injuries (Chittleborough 1974a; Aiken 1977; Ford 1977) have also been cited as factors affecting lobster growth (see Aiken 1977, Dall 1977, and Ford 1977 for a review of lobster growth). The effects of these factors are translated into growth rate variations by changing either intermolt period, molt increment, or both. Most commonly, intermolt is shortened by warm temperatures, darkness, or autotomy of appendages; and lengthened by age, cold, or low salinity. Under some conditions, as in this study, both changes in molt increment and intermolt period occurred (Mauviot and Castell 1976; Aiken 1977; Pollock and Roscoe 1977).

While autotomy may stimulate molting, Chittleborough (1974a) reported that repeated loss of two or three legs or a large number of appendages resulted in decreased molt increment, so the net result was a reduction in growth rate. The results of the current study in Biscayne Bay also clearly demonstrated the adverse impact of injuries on growth rates. However, our observations did not demonstrate any proportional relationship between the degree of injury and the degree of molt increment depression as demonstrated for shore crabs by Kuris and Mager (1975). Most injured lobsters in Biscayne Bay were missing one or both antennae and one or two legs. The growth rate of *P. argus* with these minor injuries, five or fewer missing appendages, was virtually identical to the growth rate of more seriously injured lobsters that survived and which were missing up to nine legs and both antennae. It appeared that even minor losses caused a significant shift in growth pattern.

At the mean growth rate of 0.51 mm CL/wk observed for uninjured lobsters, it took about 51 wk for a juvenile to reach the minimum legal size of 76.2 mm CL from a size of 50 mm CL at age 2 (Lewis 1951; Sweat 1968). At 50 mm CL they began to associate gregariously with the larger juveniles in the eastern bay where they were subjected to fishery pressure. At the injury-depressed growth rate of 0.31 mm CL/wk, it required 84 wk to reach legal harvest size and enter the fishery 33 wk later than uninjured lobsters. During the additional 33 wk required to reach legal harvest size, natural mortality from groupers and other predators undoubtedly eliminated significant numbers of lobsters before they could enter the fishery. Olsen and Koblic (1975) estimated natural mortality of juvenile *P. argus* in Virgin Islands National Park at 34.8%/yr, at that rate, about 22% (33/52 of annual mortality) of the injured lobsters in Biscayne Bay were lost to the fishery as a direct result of their injuries. By the end of the open season, about half of the lobsters in Biscayne Bay were missing several legs and/or antennae. The frequency of injured lobsters dropped through the 4-mo closed season to about 30%, as the population molted at least once without harrassment from fishermen (Table 1). Less than 25% of 963 juvenile lobsters examined from an unfished population at Dry Tortugas, Fla., displayed similar injuries, which were presumably due to encounters with natural predators, difficulties with molting, or other normal stresses (Davis unpubl. data). Fishery induced injuries reduced the yield per postlarval recruit by reducing growth rate and consequently allowing natural mortality to occur over a significantly longer than normal period of time.

Another aspect of injury slowed growth rates is its effect on size of maturity. Maturity in spiny lobsters is apparently more a function of age than size (Chittleborough 1974b). Therefore if growth rate is significantly reduced by fishing activities through injuries, the size of mature lobsters would be reduced in areas of intense fishing activity. In the light to moderately fished Dry Tortugas fishery, the size of first maturity of female *P. argus* was about 90 mm CL for most of the population (78 mm CL smallest ovigerous) (Davis 1975). In the intensely fished lower keys fishery, the size of first maturity was reported at about 80 mm CL (smallest ovigerous 71.4 mm CL) (Warner et al. 1977). However, while age induces onset of maturity, female size is a major limit to fecundity. Creaser (1950) pointed out that a single 130 mm CL female *P. argus* produced as many eggs as four 87 mm CL females. Under the same environmental conditions, a population of injury-stunted lobsters could not produce the number of larvae that a population of normal-sized animals would (Kanciruk and Herrnkind 1976). Spawning fewer larvae may also result in reduced genetic diversity in the *P. argus* population, which would have further detrimental consequences for the management of this valuable resource (Miller 1979).

Intense fishing pressure on commercial concentrations of spiny lobsters inflicts injuries in several ways. Recreational divers inadvertently damage juvenile lobsters in attempting to catch associated larger animals, and by repeatedly catching nearly legal-sized lobsters to measure them. Florida law permits the capture, transportation, and use of sublegal-sized juveniles for attractors (bait) in commercial traps (Florida Statute 370.14), and juveniles are occasionally caught in traps along with adults. These sources of injury to the lobsters are all amenable to standard lobster trap fishery management techniques. Escape vents on traps that would allow small lobsters to leave and a prohibition on handling and transporting juvenile lobsters could eliminate the sources of injury from the trapping segment of the fishery (Bowen 1971). Nursery sanctuaries in which no fishing activity is allowed, and regulations prohibiting the use of hooks and spears by divers could eliminate diver and trap induced injuries.

The response of *P. argus* to injuries is probably representative of most tropical palinurids, and the information developed here could have wide application for fisheries management.

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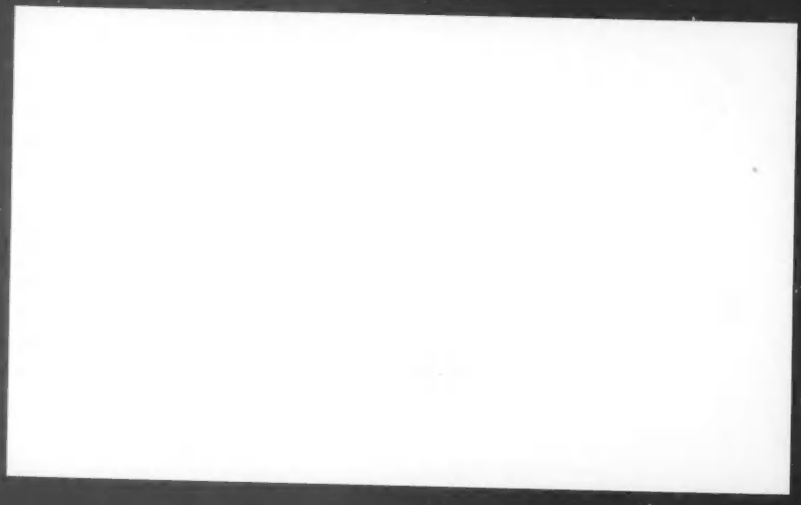

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